

BIOPHYSICAL FACTORS ASSOCIATED WITH THE MARINE GROWTH AND  
SURVIVAL OF AUKE CREEK, ALASKA COHO SALMON (*Oncorhynchus kisutch*)

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BIOPHYSICAL FACTORS ASSOCIATED WITH THE MARINE  
GROWTH AND SURVIVAL OF AUKE CREEK, ALASKA COHO  
SALMON  
(*Oncorhynchus kisutch*)

A  
Thesis

Presented to the Faculty of the University of Alaska Fairbanks  
in Partial Fulfillment of the Requirements  
for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

December 2006

ALASKA  
QL  
638  
S2  
R618  
2006



## Abstract

Correlation and stepwise regression analyses were used to investigate relationships between growth in four distinct marine habitats, marine survival, and biophysical indices for Auke Creek coho salmon, a coho salmon population in Southeast Alaska. Early marine growth of males and females were positively correlated, but neither was correlated with early marine growth of jacks. Regional biophysical indices had significant effects on early marine growth of jack, but not on early marine growth of adult coho salmon. Sea surface temperature and number of hatchery pink and chum salmon juveniles released had negative and positive effects on growth in strait habitat, respectively. Hatchery pink and chum salmon abundance and pink salmon catch in Northern Southeast Alaska were negatively related to the growth of Auke Creek coho salmon in the late ocean phase. The average length-at-return of males, but not females, was negatively related to the abundance of hatchery pink and chum salmon. Female and male size-at-return were positively correlated ( $r = 0.68$ ) but within-year variation was less for females, indicating possible sex-specific differences in adult size requirements associated with reproductive success. Adult survival and jack return rate were significantly related to early marine growth of adults and jacks, respectively, indicating size-selective mortality. Hatchery pink and chum salmon abundance had positive effects on adult survival and jack return rate.

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## **Acknowledgements**

Funding for this thesis research was provided by NOAA Fisheries Auke Bay Laboratory and the U.S. GLOBEC research program through the Cooperative Institute For Arctic Research (CIFAR) at the University of Alaska Fairbanks. It would not have been possible without the data collection efforts of the staff of NOAA Auke Bay Laboratory and the Alaska Department of Fish and Game at the Auke Creek weir. Dr. Milo Adkison of the University of Alaska Fairbanks acted as primary graduate advisor, and assisted in reviewing both data collection, statistical analysis, and thesis writing. Dr. Alex Wertheimer of NOAA Fisheries Auke Bay Laboratory and Dr. Nicola Hillgruber acted as thesis committee members and provided important advising on this project. Jerry Taylor is responsible for collecting and managing the Auke Creek coho salmon scale collection, and was immensely helpful in the collection of scale growth data for the project.



## General Introduction

This thesis investigates relationships between regional biophysical indices and scale growth of Auke Creek coho salmon (*Oncorhynchus kisutch*) within different segments of the marine life phase. Quantifying such relationships is important in understanding the mechanisms that drive variation in survival of regional salmon populations. Early marine growth of salmon is positively related to rates of survival in other populations, indicating that mortality is often size-selective during the marine life phase (Holtby et al. 1990). While large-scale climate indices such as the Pacific Decadal Oscillation are significantly related to rates of salmon survival (Hare et al 1999), regional climate indices are more synchronous with the survival rates of regional populations (Adkison et al. 1996). Regional variation in biophysical conditions in the early marine phase such as upwelling, sea surface temperature, zooplankton species diversity and abundance, precipitation, and fish species abundance can affect salmon survival in the ocean (Bax 1983; Holtby et al. 1990; Pearcy 1992; Ryding and Skalski 1999; Cole 2000; Beamish and Manhken 2001; Fukuwaka and Suzuki 2002). Fewer studies have investigated the effects of such biophysical conditions on the marine growth of individual populations (Holtby et al. 1990; Wertheimer et al. 2004).

The objectives of this thesis are (1) to characterize the growth of Auke Creek coho salmon throughout the marine life history phase, (2) to examine relationships between biophysical indices and marine growth during different segments of the marine migration, and (3) to examine relationships between biophysical indices and survival of an individual population of coho salmon, including relationships between growth and survival.

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## **CHAPTER 1: Biophysical factors associated with the marine growth and size-at-return of coho salmon from Auke Creek, Alaska<sup>1</sup>**

### **Abstract**

Correlation and stepwise regression analyses were used to investigate sex-specific and life-history-specific relationships between Auke Creek coho salmon marine growth and a suite of biophysical indices: regional sea surface temperature, precipitation, the abundance of pink and chum salmon juveniles released from a local hatchery, and pink salmon catch in Northern Southeast Alaska. Early marine growth of males and females was positively correlated, but neither was correlated with early marine growth of jacks. Male and female growth in the Gulf of Alaska and upon return to coastal regions were also positively correlated. Regional biophysical indices had significant effects on early marine growth of Auke Creek jack coho salmon, but not on early marine growth of adult coho salmon. Sea surface temperature and hatchery pink and chum salmon juvenile abundance had negative and positive effects on growth in strait habitat, respectively. Hatchery pink and chum salmon juvenile abundance and pink salmon catch in Northern Southeast Alaska were negatively related to the growth of Auke Creek coho salmon in the late ocean phase, upon return to coastal areas. The average length-at-return of male Auke Creek coho salmon was negatively related to the number of hatchery pink and chum juveniles released, but the average length-at-return of female coho salmon was not. Female and male size-at-return were positively correlated ( $r = 0.68$ ), but within-year variation was less for females, indicating possible sex-specific differences in adult size requirements associated with reproductive success.

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<sup>1</sup> Robins, J.B., M.D. Adkison, A.C. Wertheimer, and S.G. Taylor. 2006. Biophysical factors associated with the marine growth and size-at-return of Auke Creek coho salmon. Prepared for submission in Transactions of the American Fisheries Society.



## Introduction

Regional patterns of interannual variation in salmon productivity along the Pacific west coast of North America are driven by large-scale climate fluctuations (Beamish and Bouillon 1993). In particular, overall differences in survival between Pacific Northwest and Alaskan salmon stocks are related to the Pacific Decadal Oscillation (Mantua 1997; Hare et al. 1999). Indices of regional environmental conditions are more synchronous with survival patterns of individual populations than large-scale indices (Mueter et al. 2002a), and correlate significantly with population survival on small scales (800-1000 km; Mueter et al. 2002b). Mixed layer depth in the ocean, sea surface temperatures, upwelling, and wind-driven currents are examples of important conditions that regulate biological productivity in the ocean (Brodeur and Ware 1992; Polovina et al. 1995; Freeland et al. 1997; Cole 2000).

Mortality in the early marine phase of the Pacific salmon life history is an important factor in producing variation in overall survival (Parker 1971; Bax 1983; Holtby et al. 1990; Pearcy 1992; Ryding and Skalski 1999; Beamish and Mahnken 2001; Fukuwaka and Suzuki 2002). In many cases growth is the biological mechanism linking environmental variation with rates of survival. (Holtby et al. 1990; Sogard 1997; Beamish and Mahnken 2001). Many studies of climatic influences on salmon productivity have examined relationships of biophysical indices with survival; fewer have investigated relationships directly with marine growth and adult size (Holtby et al. 1990; Wells et al 2005; Wertheimer et al. 2004).

This study examines the effects of a suite of biophysical factors on inter-annual patterns of sex-specific and life-history specific scale growth for an individual population of coho salmon (*Oncorhynchus kisutch*). The primary objectives are: (1) to characterize the growth patterns of Auke Creek male, female, and jack coho salmon; (2) to investigate relationships between relevant

biological and environmental conditions and Auke Creek coho salmon growth; and (3) to ascertain the relative importance of the various biophysical factors on the different phases of growth in this population.

## Methods

### Study area

Auke Creek is the short outlet stream of Auke Lake in Southeast Alaska (58°23', 134°37'). The Auke Lake watershed contains 1072 hectares of land and is located 19.2 km north of Juneau. The lake itself has a surface area of 67 hectares and is fed by five tributaries, the largest of which is Lake Creek with a watershed of 648 hectares. Auke Lake sits at an elevation of 19 m, and is 31 m deep at its deepest point. The entire shoreline is forested, and varies from flat to steep terrain (Lum 2003). This system supports populations of pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), Chinook salmon (*O. tshawytscha*), steelhead trout (*O. mykiss*), Dolly Varden trout (*Salvelinus malma*), and cutthroat trout (*O. clarkii*) (Taylor and Lum 2003). The system produces approximately 150,000 juvenile salmonids and 24,000 adult salmonids of all species combined. On average, approximately 6000 of the juveniles and 700 of the adults are coho salmon. Pink and sockeye salmon are the most abundant species in the system, followed by Dolly Varden, chum and coho salmon, cutthroat trout, chinook salmon, and steelhead trout.

### Data sources

NOAA Fisheries Auke Bay Laboratory's Marine Salmon Interactions (MSI) group operates a two-way weir above the high-tide mark at Auke Creek.

All emigrating coho salmon smolts are captured, counted, tagged with coded wire tags (CWT), measured for fork length and weight, and released at the weir each spring. Scales, lengths, and CWTs are collected from returning adults and jacks in the fall.

NOAA Fisheries Auke Bay Laboratory's MSI group also manages the Southeast Coastal Monitoring (SECM) research project. As part of this project, surface trawls and CTD casts are conducted along the migration route of the Auke Creek coho population, namely in Icy Strait and at the entrance to the Gulf of Alaska; coded wire tagged (CWT) individuals from Auke Creek have been caught in SECM surface trawls at both the Icy Strait and Gulf of Alaska sampling stations in the past. All species recovered in trawls are identified and counted, juvenile salmon lengths are recorded, and oceanographic data are collected at each trawl station.

### **Scale growth analysis**

Scale growth data were collected from coho salmon scales sampled consistently from adult females, adult males, and jacks at Auke Creek weir since 1980. Scale impressions on acetate cards exist for scales from adult males, adult females and jack males for the smolt years 1980-2003. Scales were not collected from jack males in 1987. A previous study created images and collected growth data from adult female scales (Briscoe 2004). In 2005, under the same protocol, images of individual scales from adult males and jacks were generated using a microfiche reader with a ScreenScan scanning device connected to a desktop computer with ScreenScan software. Image contrast and resolution settings were set according to specifications recommended for coho salmon scales by the Alaska Department of Fish and Game Scale and Otolith Laboratory in Juneau, Alaska. A sample size of 20 scales per year was determined sufficient based on a power analysis. Sample sizes of 21-26 male and 15-25 jack scales were obtained



for each year of the analysis (1980-2003), and 20 female scales were obtained for each year in a previous study (except 1980, for which only 14 scales were available) (R. Briscoe, unpublished data). The sample scales were selected from available scales based on readability and scale condition. Scales in poor condition due to handling or regeneration were not used, as deformities and obscurities make circuli identification and measurement difficult or impossible. Condition of individual scales was determined based on visual inspection of scale shape (rounder scales allow the most accurate representation of somatic growth from circuli measurements), the clarity of the circuli, and the intactness of the scale's edge. Scale images were stored as digital files for subsequent analysis of growth patterns.

Adult male and jack scale growth measurements were generated following methods used for female scales by Briscoe (2004). Scale growth was measured as the sum of the widths of scale increments (circuli). Because circuli are laid down progressively over time, the pattern of circuli widths represented on a scale can be used as a proxy for somatic growth rate (Fukuwaka and Kaeriyama 1997; Fisher and Pearcy 2005). The time schedule under which circuli are produced is not well understood; however, annual growth can be identified based on the presence of regions where circuli widths are narrow (annuli). During winter, somatic growth slows and circuli become narrower than in warmer months. To achieve finer temporal resolution of growth rate, a previous study (Briscoe 2004) collected data from scales of juvenile coho caught in marine waters by surface trawl sampling (NOAA SECM project), and from those intercepted upon emigration from Auke Creek at the weir. Average circuli counts for juvenile coho salmon caught at each station were assumed to be representative of Auke Creek coho growth. Four zones of growth were identified by comparing circuli counts from scales obtained at the two stations: early marine growth, strait habitat growth, Gulf of Alaska (GOA) growth, and saltwater plus (SW plus) growth. The average number of circuli from scales collected at Icy Strait (excluding freshwater growth) was



classified as early marine growth, and the average number of circuli at the GOA stations was interpreted as strait habitat growth combined with early marine growth. Since the number of juvenile coho caught per unit of effort drops off markedly after September (Orsi et al. 2000), the average number of circuli between the endpoint of strait growth (circulus 21) and the scale annulus was treated as GOA growth. Saltwater plus growth was defined as the region from the annulus to the scale edge. Early marine, strait habitat, GOA, and SW plus growth zones were represented by the following regions on the scale: marine circuli 1-7, marine circuli 8-20, marine circuli 21- the ocean annulus, and the ocean annulus to the scale edge, respectively.

Optimas 6.51 image analysis software, employing macros written by the Alaska Department of Fish and Game, was used to standardize the measurement of circuli of individual scales to produce scale growth data. The macros identify and mark circuli along the longest axis of a scale, as defined by the user. Misclassifications were manually corrected. Using an automated measurement process, circuli widths were determined and recorded. Circuli widths were collected for 1980-2003. In order to reduce subjectivity in identification of annuli, an algorithm was devised to identify annuli from circulus width data; this consisted of finding the local minimum of circulus width between the 43rd and 73rd marine circulus, a range in which annuli are typically observed for this species and population.

Circuli width measurements were clustered into four groups according to the circuli ranges representative of the four spatio-temporal zones of marine growth: early marine, strait habitat, Gulf of Alaska (GOA), and saltwater plus (SW plus). Freshwater growth is easily distinguishable from marine growth by the smaller circuli widths, and was excluded from this analysis. In order to reduce subjectivity due to observer differences, an algorithm was devised to find the circulus at which freshwater growth ends and saltwater growth begins by identifying the maximum difference between averages of adjacent groups of three

circulus widths for an individual sample scale. For individual scales, circuli widths in each zone were added to get zone widths, and then zone widths were averaged over all scale samples in each year to produce average annual zone widths.

### **Environmental and biological indices**

Several environmental and biological indices were compared to scale growth data. The environmental indices were Auke Bay sea surface temperature (SST), Icy Strait air temperature, Auke Bay precipitation, and the Pacific Decadal Oscillation (PDO, sea surface temperature anomalies). The biological indices were Auke Creek coho salmon average smolt length, Auke Creek coho average adult fork length, DIPAC hatchery releases of pink and chum salmon fry, and pink salmon catch in the northern portion of Southeast Alaska (ADF&G districts 109-115). Correlation coefficients were calculated for all pairwise comparisons between biophysical indices and the most relevant scale growth zones. In the following, all indices are described in terms of the data source and potential relevance to coho salmon growth.

#### **Auke Bay sea surface temperature (SST)**

Daily SST measurements recorded at the Auke Bay dock (Wing et al. 2006) were averaged for the months of May and June for each year between 1979-2003. Regional SST may influence juvenile coho salmon indirectly by regulating productivity in marine waters and directly by increasing the growth potential of the fish at higher temperatures within their tolerance range (e.g., Brett 1969). Productivity can be nutrient-limited (Polovina et al. 1995). Other studies

have shown that SST is significantly correlated with salmon growth on a regional spatial scale (Mueter et al. 2002a, b).

### **Icy Strait air temperature index**

An index of air temperature was generated from data collected at Hoonah, Gustavus, and Elfin Cove, Alaska, and used as a proxy for SST in Icy Strait following the approach of Adkison et al (1996). This index was created by subtracting the monthly mean air temperature over the years 1979-2002 (National Weather Service, <http://pajk.arh.noaa.gov/climatology/webcli.htm>) from monthly average air temperatures for each year to obtain residuals. Residuals were then divided by the standard deviation of the monthly air temperatures for all years. This was performed for each of the three sites, for July, August, and September, the months during which juvenile salmon would be expected to inhabit strait habitat. Values for the three months were then averaged for each site, and site values were again averaged to obtain the overall summer habitat air temperature index for Icy Strait (Briscoe 2004). Icy Strait air temperature might be expected to affect the growth of larger juvenile coho salmon from Auke Creek, represented by the strait growth region of the scale.

### **Auke Bay precipitation**

The index for Auke Bay monthly precipitation was generated for the years 1979-2003 by measuring monthly total precipitation and averaging totals for each month over all years (Wing et al. 2006). Precipitation influences productivity in marine waters through formation of a freshwater lens, resulting in stratification of the water column (Mann and Lazier 1991). Stratification following mixing generally results in higher primary and secondary productivity. Because zooplankton are important food resources for juvenile salmon in marine regions,

changes in their abundance can potentially affect rates of salmon growth and subsequent survival.

### **Pacific Decadal Oscillation (PDO)**

PDO index values are essentially SST anomalies. For this study we used sums of the October-February North Pacific Ocean SST anomalies for the years 1980-2003, taken from Mantua et al. (1997) (<http://jisao.washington.edu/pdo/PDO.latest>) . These months represent the initial period of Auke Creek juvenile coho salmon residence in the Gulf of Alaska, during which high pre-winter mortality due to cold and nutrient-poor conditions would be expected (Beamish and Mahnken 2001). Because the PDO index incorporates data for the entire North Pacific Ocean, it represents temperature conditions on a large spatial scale.

### **Abundance of DIPAC hatchery pink and chum fry**

The number of pink and chum salmon fry produced each year at the DIPAC hatchery, which is located only a few kilometers from Auke Creek in Juneau, Alaska, are estimated prior to release into marine waters (R. Focht, unpublished data). The abundance of these pink and chum fry could be negatively correlated with the growth of Auke Creek coho salmon due to density-dependent competition for food resources. It also could be positively correlated with Auke Creek coho growth if hatchery fry serve as a buffer to predation upon Auke Creek smolts, or if hatchery fry add to the available food resources of Auke Creek coho juveniles.



### **Auke Creek coho smolt length**

Fork lengths of all Auke Creek coho smolts are measured at the weir on Auke Creek each year. The length of coho smolts upon emigration from Auke Creek may influence subsequent growth. Other studies have documented the influence of size on survival in salmonid fishes (Sogard 1997). In general, theory holds that fish of larger size will be more successful in avoiding predators (Bilton et al. 1982; Holtby et al. 1990). Smolt size is not necessarily correlated with adult size. In the jack life history, smolts that become jacks initially grow fast and are larger as smolts, but as mature jacks are small in relation to mature adults (Rowe and Thorpe 1990; Lum 2003).

### **Commercial pink salmon catch in Northern Southeast Alaska**

Alaska Department of Fish and Game commercial pink salmon catch totals for Northern Southeast Alaska were obtained for the years between 1980-2003 (Byerly et al. 1999; L. Shaul, unpublished data). The abundance of adult pink salmon could be negatively related to coho salmon survival if competition for food resources limits growth in the Gulf of Alaska. Run-timing of pink and coho salmon in this region are similar enough that such a mechanism is plausible.

### **Auto-correlation and normality of data**

All data sets were tested for lag 1 auto-correlation to determine whether tests of significance required correction (Pyper and Peterman 1998). Data sets were also examined for normality using visual inspection of frequency histograms and P-P plots, and transformed if necessary.

## Correlation analyses

Correlation analyses were performed to examine relationships between scale growth with regional environmental conditions and biological indices. This was done only for those cases where a biologically plausible mechanism existed for the effect of a variable on location-specific growth. Correlations between the growth of males, females, and jacks were also calculated for each growth region. Peterson correlation coefficients were calculated using the Correl() function in Microsoft Excel, and statistical significance was assessed using critical values of the correlation coefficient  $r$  (Zar 1999). For correlations that were statistically significant, data were visually examined for outliers to minimize the potential for erroneous results.

## Model Selection

Model selection was conducted using multiple regression models to examine the relationship between biophysical parameters to marine scale growth. In order to test the effects of environmental and biological phenomena on the response variables of interest, corrected Akaike Information Criterion (AICc) values were calculated for all possible models for a given growth zone. AICc values were calculated as:

$$AIC + \frac{2P(P+1)}{N - P - 1},$$

where AIC is determined by the following formula:

$$AIC = N * \log(RSS/N) + 2P + \text{constant}$$

where RSS is the residual sum of squares of the model, N is the number of samples, and P is the number of parameters in the model.

The best model was defined as that having the lowest AICc value. Other models with an AICc value within 2 are almost equally plausible (Burnham and Andersen 2002). AICc is used instead of the uncorrected AIC statistic in situations where sample sizes are low.

The response variables of interest in this case are early marine, strait habitat, GOA, and SW plus growth of males and females, early marine growth of jacks, and size-at-return of both males and females; a total of 11 response variables of interest.

The full model for early marine growth of both adults and jacks is:

$$G_{EM} = \alpha + \beta T_M + \beta T_J + \beta P_M + \beta P_J + \beta D_{PC} + \beta L_S$$

where  $T_M$  and  $T_J$  are Auke Bay sea surface temperature in May and June respectively,  $P_M$  and  $P_J$  are Auke Bay precipitation in May and June respectively,  $D_{PC}$  is the abundance of pink and chum salmon fry released from DIPAC Hatchery, and  $L_S$  is the average fork length of emigrating smolts.

The full model for strait habitat growth is:

$$G_{IS} = \alpha + \beta T_{IS} + \beta D_{PC} + \beta L_S$$

where  $T_{IS}$  is the Icy Strait air temperature index,  $D_{PC}$  is the abundance of pink and chum salmon fry released from DIPAC Hatchery, and  $L_S$  is the average fork length of emigrating smolts.

The full model for GOA growth is:

$$G_{GOA} = \alpha + \beta T_{PDO} + \beta D_{PC} + \beta C_{NS}$$

where  $T_{PDO}$  is the index of the Pacific Decadal Oscillation,  $D_{PC}$  is the abundance of pink and chum salmon fry released from DIPAC Hatchery, and  $C_{NS}$  is Northern Southeast Alaska pink salmon catch.

The full model for SW plus growth is:

$$G_{SWP} = \alpha + \beta T_{PDO} + \beta D_{PC} + \beta C_{NS}$$

where  $T_{PDO}$  is the index of the Pacific Decadal Oscillation,  $D_{PC}$  is the abundance of pink and chum salmon fry released from DIPAC Hatchery, and  $C_{NS}$  is Northern Southeast Alaska pink salmon catch.

The full model for size-at-return is:

$$L_R = \alpha + \beta G_{EM} + \beta G_{IS} + \beta G_{GOA} + \beta G_{SWP} + \beta T_{PDO} + \beta D_{PC} + \beta C_{NS}$$

where  $G_{EM}$  is early marine growth,  $G_{IS}$  is strait habitat growth,  $G_{GOA}$  is Gulf of Alaska growth,  $G_{SWP}$  is saltwater plus growth,  $T_{PDO}$  is the index of the Pacific Decadal Oscillation,  $D_{PC}$  is the abundance of pink and chum salmon fry released from DIPAC Hatchery, and  $C_{NS}$  is Northern Southeast Alaska pink salmon catch.

Since each full model has between 3-7 biologically relevant predictor variables to test for inclusion, stepwise model selection was performed using the “step” and “lm” functions in the statistical software package R (CRAN project; <http://cran.r-project.org/>). The stepwise model selection procedure started with a full model,



sequentially removed and re-added individual parameters to account for all possible parameter combinations, and arrived at the model with the lowest AICc value. The R procedure is based on the AIC statistic; models selected using R were examined to ensure that they would have also have been selected using the AICc criterion.

## **Results**

### **Data collection**

There was no significant difference in the average total number of marine? circuli between male (78) and female scales (77) (t-test,  $p=0.0000087$ ). The average total number of circuli on jack scales (49) was substantially lower than on adult scales because the life span of jacks is shorter than that of adults. Average total scale widths were significantly different between males and females (t-test,  $p=0.09$ ) with females being larger than males. Jack scale widths were substantially smaller than both females and adult males due to the jack life history (Table 1). The yearly averages of marine zonal growth for the smolt years 1980-2003 are presented in Table 1.1 and Figures 1.1-1.4. Because many individual jack scales have fewer than 20 saltwater circuli, the yearly averages for strait habitat growth of jacks (circulus 8 – circulus 20) are biased low (Figure 1.2).

The average length-at-return of Auke Creek coho salmon differed significantly between adult males and females (paired t-test,  $p=0.027$ ) (Figure 1.5). Over 24 years, females were on average 10mm larger than males. The average standard deviation of females (50 mm) was significantly less than that of males (38 mm) (paired t-test;  $p=0.000000034$ ).

## **Correlation analyses**

### **Auto-correlation and normality of data**

Significant positive auto-correlation was detected in the DIPAC hatchery pink and chum release abundance data. No other data sets used in correlation analyses showed significant auto-correlation. Since auto-correlation only presents problems when both arrays in a pairwise correlation analysis are auto-correlated, there was no need to adjust degrees of freedom in any case (Pyper and Peterman 1998).

No outliers were found in any of the data sets. No data sets showed significant deviation from a normal distribution, based on frequency histograms and P-P plots.

### **Male, female, and jack scale growth correlations**

Scale growth of males and females was significantly correlated in the early marine, GOA, and SW plus growth zones, but not in the strait habitat zone. Male and female scale growth were not significantly correlated with jack growth (Table 2).

### **Biophysical correlations with scale growth: early marine growth**

No significant correlations were detected between early marine growth of Auke Creek coho salmon and associated biophysical variables (Table 3). The growth of jacks and adults tended to have opposing relationships with these variables. Auke Bay SST in May was negatively correlated with male and female early marine growth, and positively with that of jacks. Auke Bay SST in June was also negatively correlated with early marine growth of jacks. Auke Bay

precipitation in May was positively correlated with male and female early marine growth, but negatively with that of jacks (Table 3).

### **Model selection: early marine growth**

The best model of male Auke Creek coho early marine growth, according to the value of AICc, contained only one variable: the number of DIPAC hatchery pink and chum released. However, the  $R^2$  value (0.074) for this model indicates that it explains little of the total variation in the data (Table 4). An equally good model (i.e., AICc within 2) contained two variables: the abundance of DIPAC hatchery pink and chum released, and June Auke Bay SST, but also explained less than 8% of the variation in growth (Table 4).

The best model of female Auke Creek coho early marine growth contained one variable: June Auke Bay SST. However, this model likewise did not explain much of the variation ( $< 1\%$ ) in the data (Table 5). An equally good model contained two parameters: June Auke Bay SST and the average length of Auke Creek coho smolts. This model also explained only 1.1% of the variation in growth according to the  $R^2$  value (Table 5).

The best model for jack Auke Creek coho early marine growth contained one parameter: June Auke Bay SST. An equally good model contained an additional parameter for June Auke Bay precipitation (Table 6). These models for jack early marine growth were better fits than the models for adult early marine growth, but still explained less than 15% of the variation in growth according to the  $R^2$  values (Table 6; Figure 1.1).

### **Biophysical correlations with scale growth: strait habitat growth**

Significant and non-significant relationships were detected between strait habitat growth and biophysical indices (Table 7). Correlations of Auke Creek

coho growth in strait habitat with the Icy Strait air temperature index were negative, but were not statistically significant. A significant positive relationship was detected between strait habitat growth of Auke Creek coho males and females and the abundance of DIPAC hatchery pink and chum smolts (Table 7).

### **Model Selection: strait habitat growth**

The best model of male strait habitat growth contained one parameter: the abundance of DIPAC hatchery pink and chum released. An equally good model contained two parameters: the abundance of DIPAC hatchery pink and chum released, and Icy Strait air temperature (Table 8). These models explained around 20% of the variation in male strait habitat growth.

The best model of female strait habitat growth contained two parameters: the abundance of DIPAC hatchery pink and chum released, and the average length of Auke Creek coho smolts. This model explained 34% of the variation in female strait habitat growth. There were two other possible models that were equally good (Table 9; Figure 1.2).

### **Biophysical correlations with scale growth: Gulf of Alaska growth**

No significant correlations were detected between the GOA growth of Auke Creek coho salmon and the associated biophysical parameters (Table 10). No significant correlation was detected between GOA growth and either hatchery release abundance or Northern Southeast Alaska (NSEAK) pink catch. Correlations with the PDO index were positive for male GOA growth, and negative for female GOA growth, but were not statistically significant (Table 10).



**Model Selection: Gulf of Alaska growth**

The best model of male GOA growth contained a single parameter: Northern Southeast Alaska pink salmon catch. None of the models selected using the AICc criterion explained more than 7% of the variation in the data according to  $R^2$  values (Table 11).

The best model of female GOA growth contained a single parameter: the abundance of DIPAC hatchery pink and chum released. An equally good model contained an additional parameter for the PDO index (Table 12). These models explained only 6% to 8% of the variation in GOA growth (Figure 1.3).

**Biophysical correlations with scale growth: saltwater plus growth**

Saltwater growth of both sexes was positively related to the PDO, and negatively related both to hatchery releases of pink and chums and to the catch of pink salmon (Table 13). However, only the correlation between male growth and PDO, and between female growth and hatchery pink and chum releases were statistically significant.

**Model Selection: saltwater plus growth**

The best model of male saltwater plus growth contained two parameters: the PDO index and NSEAK pink salmon catch. Two other models were equally good according to AICc values, and explained significant amounts of the variation in the data (Table 14). One contained an additional parameter for the abundance of DIPAC hatchery pink and chum released, and the other contained a single parameter for the PDO index. These models explained 27% to 42% of the variation in male plus growth.

The best model of female marine plus growth contained two parameters: the abundance of DIPAC hatchery pink and chum released, and NSEAK pink catch. An equally good model contained an additional parameter for the PDO index (Table 15). These models explained 15% to 17% of the variation in female plus growth (Figure 1.4).

### **Biophysical correlations with size-at-return**

Male and female size-at-return were positively, but not significantly correlated with early marine growth of males and females respectively. Correlations between male size-at-return and both strait and GOA growth were not significant and negative. Correlations between female size-at-return and both strait and GOA growth were not significant and positive. Male size-at-return was positively and significantly correlated with SW plus growth and with the PDO index. Female size-at-return was positively, but not significantly correlated with female SW plus growth and the PDO index. Male and female size-at-return were negatively, but not significantly correlated with the abundance of DIPAC hatchery pink and chum salmon releases, and NSEAK pink salmon catch. Female size-at-return was positively and significantly correlated with male size-at-return (Table 16).

### **Model selection: size-at-return**

The best model of male size-at-return included one parameter: the PDO index. An equivalently good model included two additional parameters for male SW plus growth and the abundance of DIPAC hatchery pink and chum salmon released. Both models explained over 50% of the variation in the data as indicated by  $R^2$  values (Table 17).

The best model of female size-at-return included two parameters: the PDO index and female SW plus growth. An equivalently good model included an additional parameter for female GOA growth. These models explained 20% to 23% of the variation in the data as indicated by  $R^2$  values (Table 18; Figure 1.5).

## Discussion

We found several important relationships between Auke Creek coho salmon scale growth and marine biophysical conditions. The marine growth of male and female coho salmon were significantly correlated with each other in three of the four regions (all except strait habitat), but not with the early marine growth of jacks. These results imply differences between the growth patterns of individuals with an adult life history and those with a jack life history. Positive correlations between male and female growth during most of the marine life history of Auke Creek coho salmon over twenty-four years imply that males and females experience similar environmental conditions at sea. The lack of significant correlations between Auke Creek male and female coho salmon growth in strait habitat may indicate sex-specific differences in growth patterns during the period when Auke Creek coho salmon are assumed to be migrating through Icy Strait.

Regional biophysical indices were generally not related to the early marine growth of adult-type coho salmon. However, the same indices explained more variation in jack-type coho salmon early marine growth. The lack of a significant relationship between early marine growth of adult-type juvenile salmon and the abundance of hatchery releases is surprising in light of hypotheses about the potential density dependent effects of hatchery-released pink and chum fry on the growth of wild fry during early marine rearing (Ruggerone and Nielsen 2004; Wertheimer et al. 2004). It suggests that a negative density-dependent effect of

hatchery pink and chum salmon juvenile abundance effect on coho salmon growth does not occur during initial marine rearing. This may be due to hatchery releases not remaining long in Auke Bay at high densities, or because spring productivity in subarctic ecosystems is high enough that competition for food resources does not occur at these densities.

Biophysical factors in Auke Bay have a more pronounced effect on growth of jacks than adult-type coho salmon, indicating that the jacks may reside longer in Auke Bay than juveniles of adult-type coho salmon. Adult-type salmon may move offshore soon after entry, while jacks remain more coastally oriented due to their short marine phase. SST in Icy Strait is positively correlated with SST in Auke Bay ( $r = 0.48$ ), so even if adult-type salmon migrate to Icy Strait, they likely experience thermal conditions similar to Auke Bay. Other biophysical factors such as currents and zooplankton abundance between Auke Bay and Icy Strait may be responsible for the life-history specific differences in relationships between early marine growth and biophysical factors. The stronger relationship of jack growth to local environmental conditions is supported by other evidence that Auke Bay SST is more significantly correlated with return rate of jacks than with survival of adults (Briscoe et al. 2005).

While the regional biophysical indices used in this study did not explain much of the variation in early marine growth of Auke Creek adult coho salmon, strong relationships between growth and environmental indices have been found in other populations. Regional coastal upwelling was positively correlated with early ocean growth over seventeen years for a population of coho salmon in Southern British Columbia (Holtby et al. 1990). Mixed layer depth during the early marine phase had the strongest relationship to adult size in Puget Sound hatchery coho salmon populations, compared with a suite of environmental indices (Hobday and Boehlert 2001).

In the strait habitat zone, growth of males and females was positively related to the abundance of DIPAC hatchery pink and chum salmon releases, and



negatively related to air temperature. The negative relationship of adult-type coho salmon growth in strait habitat to Icy Strait air temperature is in contrast to the positive relationship between jack growth and Auke Bay SST in the early marine phase. Positive relationships between growth and water temperature would be expected. Growth of juvenile salmon is typically positively correlated with local water temperature (Brett 1969; Mortenson et al. 2000) and often precipitation (Mann and Lazier 1991). It may be that the negative relationship between growth and SST in Icy Strait is indirect. Biophysical factors associated with decreasing temperatures, such as increased nutrient concentrations or mixed layer depths due to upwelling or currents, may have a positive influence on growth (Brodeur and Ware 1992; Polovina et al. 1995; Hobday and Boehlert 2001).

No sufficient regional index of coastal upwelling was available for this study. Large differences in environmental indices between the early marine and strait habitat regions would not be expected, however, due to their close proximity. Mueter et al (2002b) found that correlations with salmon survival were strongest for regional environmental conditions (SST and coastal upwelling) over areas of less than 1000 kilometers.

Oceanographic processes can limit food availability in turn limiting juvenile growth despite favorable water temperatures (Logerwell et al. 2003; Wells et al. 2006). Shifts in ocean currents associated with climatic influences can produce variation in the spatial distribution of marine nutrient concentrations (Polovina et al. 1995; Freeland et al. 1997). In particular, fluctuation in the depth of the ocean mixed layer can affect timing and quantity of primary productivity. In subarctic regions, a shallow ocean mixed layer is generally associated with higher primary productivity (Polovina et al. 1995).

Regional climate patterns can also limit primary productivity. In Prince William Sound, stormy spring weather results in continuous mixing of the surface layer which replenishes nutrient concentrations, allowing zooplankton productivity to remain high. In warm springs with fewer storms, less mixing

occurs, and productivity of phytoplankton and zooplankton become limited (Eslinger et al. 2001). Hobday and Boehlert (2001) showed a weak positive effect of SST on coho salmon growth in the Pacific Northwest, but a stronger positive effect of mixed layer depth.

Though salmon are typically opportunistic foragers, diet preferences for certain zooplankton species have been shown to exist (Healey 1986; Brodeur and Pearcy 1990; Armstrong et al. 2005; Kaeriyama et al 2004). Salmon productivity can be limited when the species composition and overall abundance of zooplankton prey resources are limited (Willette 1999; Cooney et al. 2001; MacFarlane et al 2005).

Top-down, as well as bottom-up processes can be expected to influence growth of juvenile coho salmon. The abundance, temporal and spatial distribution of predators likely play a role in regulating juvenile salmon growth, by influencing the risks associated with foraging. Juvenile salmon are known to alter foraging patterns in response to predation. Juvenile sockeye salmon rearing in lakes have a diel vertical migration pattern in order to avoid predation (Scheuerell and Schindler 2003), whereas the less risk-averse strategy of juvenile pink salmon apparently involves foraging diurnally in surface waters to achieve rapid growth rates (Godin 1984; Robins et al. 2005).

Capturing the variation in predator dynamics is difficult, and a paucity of data on distribution and consumption rates exists. Food web modeling has been conducted to investigate predator population dynamics (Aydin et al. 2005; Field et al. 2006). Hydroacoustic surveys have been used to quantify the abundances of organisms of different sizes, which can be useful in exploring food web dynamics (Swartzman et al. 2003; Gauthier et al. 2004). While some of the predators of juvenile salmon in Northern Southeast Alaska are commonly known, data on abundances of each are difficult to obtain. No sufficient index of predator abundance was available to assess top-down influences on Auke Creek juvenile salmon growth.

The positive relationship with hatchery release abundance is possibly due to predation buffering from hatchery pink and chum salmon in the strait habitat region. If coho experience less intense predation because predators are foraging on pink and chum hatchery smolts, they will expend less energy avoiding predators, and can allocate this towards growth. It is unlikely that juvenile coho consume juvenile pink or chum salmon in strait habitats, due relatively small size differences between juveniles of the three species when they commingle in the strait habitat (J. Orsi, personal communication). Because many populations of salmon have mixed by the time Auke Creek coho salmon have reached strait habitat, the effect of a single hatchery population is unlikely to be solely responsible for a positive effect on coho salmon growth. If DIPAC hatchery release abundance is positively correlated with the abundance of pink and chum salmon juveniles in NSEAK, the DIPAC index may essentially be a proxy for pink and chum salmon juvenile abundance, but this has not been investigated to date. Therefore, this result may be spurious.

Variation in the growth of males and females in the Gulf of Alaska was not significantly explained with any of the models tested. Salmon production in Alaska varies inversely with that of the Pacific west coast on a 20-30 year cycle (Hare et al. 1999). The positive phase of the PDO indicates low pressure and upwelling in the central GOA, which improves productivity in that region and translates to increased growth of salmon there (Mantua et al. 1997; MacFarlane et al. 2005; Scheurell and Williams 2005). Positive PDO has the opposite effect on salmon populations further south due to decreased upwelling offshore (Mantua et al. 1997). In some cases coastal downwelling can increase productivity in nearshore marine regions through advection of zooplankton (Brodeur and Ware 1992), which might be expected to result in increased early marine growth of salmon. In general, regional environmental indices have been shown to explain variation in salmon productivity better than large-scale indices (Mueter et al. 2002a). The fact that models of Gulf of Alaska growth in this study did not



explain significant variation in the data implies that the biophysical indices used in the analysis of Gulf of Alaska growth data were unrelated to growth during this phase.

The growth of male and female coho salmon in the saltwater plus growth zone was positively related to the PDO index, but less so for females. Growth of males and females in the saltwater plus growth zone was negatively related to the abundance of DIPAC hatchery pink and chum salmon releases and NSEAK pink catch. The negative relationships between saltwater growth and the two indices of pink salmon abundance indicate potential density-dependent relationships late in the marine phase of the coho salmon life history. Coho salmon feed at a higher trophic level than pink salmon during initial marine residence because they enter marine waters having grown to larger sizes during freshwater residency. However, pink salmon grow more rapidly than other salmon species (Godin 1981) and the overlap in coho and pink salmon diets likely increases with the average size of juvenile pink salmon (Brodeur 1990; Ruggerone and Nielsen 2004).

Catch abundance of NSEAK pink salmon was positively correlated with NSEAK coho salmon catch, and with Auke Creek adult coho salmon survival (Briscoe et al 2005), further supporting the hypothesis that pink and chum salmon abundance may partially regulate growth and survival of Auke creek coho salmon. In Southwest Alaska and in the Puget Sound, negative impacts of pink salmon abundance on the growth, survival, and age-at-maturity of sympatric species of salmon have been documented (Ruggerone et al. 2003; Ruggerone and Nielsen 2004; Ruggerone and Goetz 2004). Pink salmon size-at-return is negatively related to pink salmon abundance in Prince William Sound, Alaska (Wertheimer et al. 2004). The positive relationships with PDO imply that large-scale conditions affecting the Gulf of Alaska have a positive influence on late ocean growth of Auke Creek coho salmon.

Both male and female size-at-return were positively related to the PDO index. Only male size-at-return was negatively related to the abundance of

DIPAC hatchery pink and chum salmon releases. Male and female size-at-return were positively related to male and female saltwater plus growth, respectively; only female size-at-return was positively related to Gulf of Alaska growth. The positive relationship between size-at-return and saltwater plus growth for both male and females implies that size-at-return is largely determined during the saltwater plus growth phase. The non-significant correlations between size-at-return and both early marine and strait growth for males and females implies that growth during these periods has little effect on size-at-return.

The positive relationship between both male and female size-at-return and the PDO index indicates that size is positively affected by positive PDO anomalies, which result in higher temperatures and increased upwelling in the central Gulf of Alaska. This interpretation is supported by the finding that female size-at-return is positively related to female Gulf of Alaska growth, and by the insignificant positive correlation between female GOA growth and the PDO index. These results contrast with those of another recent study that showed a negative relationship between PDO and the adult size at return for Alaska coho populations (Wells et al. 2006).

Trends in size-at-return of males and females are positively correlated, but the average size-at-return of females is significantly greater than that of males over twenty-four years. While intrinsic sex-specific differences exist, the strong positive relationship between male and female size-at-return implies an overall environmental influence on growth. However, female coho salmon size-at-return also varies significantly less than that of males. The greater average size of females, coupled with the lesser amount of variation in female size, implies that growth of females is constrained by size requirements in some way. Body size of female salmon is positively related to reproductive success. Larger females can produce larger and more numerous eggs (van den Berghe and Gross 1989; Hendry et al. 2001; Kinnison et al. 2003). The lesser amount of variation in female size-at-return, as compared with that of males, supports the hypothesis that there is a

threshold size at which females can produce viable and sufficiently numerous eggs.

Female coho salmon may forage more aggressively than males to achieve more stringent size requirements for reproductive success (Healey 1986; Holtby and Healey 1990). Male salmon can successfully reproduce at a variety of sizes, via different life history strategies (Gross 1985). There is evidence that male size does not affect their fertility or pose direct advantages for offspring in chinook salmon (Berejikian and Tezak 2005). The results of this study indicate that hatchery pink and chum salmon abundance has a negative effect on size-at-return of males and females. The catch abundance of pink salmon in Northern Southeast Alaska has a negative effect on the size-at-return of males, but a positive effect on that of females. In foraging more aggressively, female coho salmon may effectively mitigate for any negative density-dependent effect from pink salmon during the late ocean phase, whereas males may not require such mitigation to insure reproductive success.

The results presented here suggest that early marine biophysical conditions may be more influential on growth and size of coho salmon with a jack life history. In general, male and female coho salmon growth are positively correlated throughout the marine phase of life. Air temperature in Icy Strait is negatively related to coho salmon growth during residence in this region, implying that colder temperatures improve productivity in this region; however, increases in nutrient concentrations associated with local upwelling may be responsible. The index of Pacific Decadal Oscillation is positively related to late ocean growth in males and females, implying that upwelling in the central Gulf of Alaska positively benefits ocean growth of Auke Creek coho salmon. Indices of pink salmon abundance are negatively correlated with late ocean growth of coho salmon, indicating potential density-dependent effects on growth. This effect is also reflected in relationships between pink salmon catch and size-at-return for female, but not male salmon. Average female size-at-return is significantly



greater than that of males, and exhibits less variation, supporting the hypothesis that sex-specific differences in foraging occur.

One limitation of this study is that scales were available only from the fish that survived to return to the Auke Creek weir. Surviving salmon likely grew faster than average as juveniles (Beamish and Mahnken 2001; Moss et al. 2005). Despite this bias in the available samples, any environmentally- or biologically-driven interannual differences in growth rates should still be evident in the growth data, although possibly less pronounced.

Future studies of Auke Creek salmon growth should investigate appropriate indices of regional primary and secondary productivity for use in correlation analyses and modeling. An index for juvenile pink salmon abundance in NSEAK would be useful in clarifying the influence on coho salmon early marine growth. A study similar to this, but considering growth data for several populations of coho salmon in Southeast Alaska would be useful in exploring how responses to biophysical indices vary spatially on a regional scale. Incorporating an index of abundance for forage fishes which use the same pelagic and nearshore habitats as juvenile salmon may be an effective way to analyze density-dependent effects on Auke Creek juvenile coho growth (Ware and McFarlane 1988; Holtby et al. 1990). Given the high annual adult survival rate of Auke Creek coho salmon (average = 20 %), an acoustic telemetry study to ascertain the range and spatial distribution of Auke Creek coho jack-type salmon would be possible. This could provide the basis for an analysis of the effects of regional biophysical conditions on jack growth on an especially small scale.

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Table 1.1: Average scale growth (mm) over all years of data (1980-2003) for zonal growth regions.

	M	F	J
Early marine	0.32	0.28	0.49
Strait	0.71	0.73	0.53
GOA	0.57	0.69	na
SW Plus	1.40	1.35	na
Total	3.45	3.51	1.73

Table 1.2: Correlation coefficients for relationships between Auke Bay, Strait habitat (Strait), and Gulf of Alaska (GOA) growth of Auke Creek coho females and males (F=Female, M=Male, J=Jack). Values in bold font are statistically significant. Asterisks indicate the two-tailed level of significance: (\* <0.05, \*\* <0.025, \*\*\* <0.01).

	Early Marine			Strait			GOA		SW Plus	
	F	M	J	F	M	J	F	M	F	M
F	1.00	<b>0.63***</b>	0.05	1.00	0.01	-0.29	1.00	<b>0.50**</b>	1.00	<b>0.69***</b>
M	<b>0.63***</b>	1.00	0.10	0.01	1.00	-0.34	<b>0.50**</b>	1.00	<b>0.69***</b>	1.00
J	0.05	0.10	1.00	-0.29	-0.34	1.00	NA	NA	NA	NA



Table 1.3: Correlation coefficients for analyses of relationships between early marine growth and environmental/biological indices. Values in bold font are statistically significant. Asterisks indicate the two-tailed level of significance: (\* <0.05, \*\* <0.025, \*\*\* <0.01).

	Female	Male	Jack
AB May SST	0.02	0.26	-0.05
AB June SST	0.08	0.07	-0.36
AB May Precip	-0.20	-0.25	0.13
AB June Precip	0.09	0.03	0.18
Hatchery pink/chum	0.04	0.27	0.06
Smolt length	0.10	0.12	-0.14

Table 1.4: Models of male Auke Creek coho early marine growth and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	May SST	May precip	June SST	June precip	Pink/chum	Smolt length	AICc	R <sup>2</sup>
0.4211	0.0002	-0.0035	-0.0019	-0.0014	1.68E-10	0.0006	-184.30	0.1577
0.4201		-0.0035	-0.0018	-0.0014	1.73E-10	0.0006	-187.91	0.1576
0.4110			0.0006	0.0006	1.77E-10	0.0002	-190.99	0.07962
0.4126			0.0001		1.74E-10	0.0003	-193.73	0.07715
<b>0.4417</b>			<b>0.0005</b>		<b>1.81E-10</b>		<b>-196.21</b>	<b>0.07436</b>
<b>0.4481</b>					<b>1.84E-10</b>		<b>-196.78</b>	<b>0.07386</b>

Table 1.5: Models of female Auke Creek coho early marine growth and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	May SST	May precip	June SST	June precip	Pink/chum	Smolt length	AICc	R <sup>2</sup>
0.3638	-0.0032	-0.0031	0.0018	0.0004	8.66E-11	0.0008	-183.28	0.0855
0.3652	-0.0032	0.0015	0.0015		8.44E-11	0.0008	-186.87	0.08478
0.3744	-0.0007		0.0013		2.62E-11	0.0004	-189.98	0.01366
0.3718	-0.0004		0.0013			0.0005	-192.61	0.01247
<b>0.3758</b>			<b>0.0011</b>			<b>0.0004</b>	<b>-194.81</b>	<b>0.01147</b>
<b>0.4144</b>			<b>0.0016</b>				<b>-196.90</b>	<b>0.006111</b>

Table 1.6: Models of jack Auke Creek coho early marine growth and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	May SST	May precip	June SST	June precip	Pink/chum	Smolt length	AICc	R <sup>2</sup>
0.6946	0.0022	0.0039	-0.0093	0.0039	6.03E-11	-0.0012	-163.08	0.2012
0.6907	0.0029	0.0041	-0.0094	0.0038		-0.0011	-166.60	0.1981
0.5969	0.0020	0.0032	-0.0110	0.0031			-169.29	0.1793
0.6017		0.0027	-0.0098	0.0034			-171.94	0.1698
<b>0.6348</b>			<b>-0.0109</b>	<b>0.0019</b>			<b>-173.80</b>	<b>0.1417</b>
<b>0.6516</b>			<b>-0.0116</b>				<b>-175.81</b>	<b>0.1274</b>

Table 1.7: Correlation coefficients for analyses of relationships between Strait habitat growth and environmental/biological indices. Values in bold font are statistically significant. Asterisks indicate the two-tailed level of significance: (\* <0.05, \*\* <0.025, \*\*\* <0.01).

	Female	Male	Jack
Icy Str. AT	-0.05	-0.11	0.36
PDO (Oct-Feb)	0.17	-0.05	-0.16
Hatchery pink/chum	<b>0.48**</b>	<b>0.44*</b>	0.23
Smolt length	0.10	-0.22	-0.30



Table 1.8: Models of male Strait habitat growth and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	Icy Strait AT	Hatchery pink/chum	Smolt length	AICc	R <sup>2</sup>
0.6234	-0.0046	5.27E-10	0.0002	-168.17	0.2112
0.6465	-0.0048	5.34E-10		-170.79	0.2108
<b>0.6466</b>		<b>5.29E-10</b>		<b>-172.72</b>	<b>0.1957</b>

Table 1.9: Models of female Strait habitat growth and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	Icy Strait AT	Hatchery pink/chum	Smolt length	AICc	R <sup>2</sup>
1.0340	-0.0053	6.19E-10	-0.0032	-178.33	0.3665
1.0010		6.06E-10	-0.0029	-180.15	0.3449
0.6703		5.20E-10		-178.72	0.2318

Table 1.10: Correlation coefficients for analyses of relationships between Gulf of Alaska (GOA) growth and environmental/biological indices. Values in bold font are statistically significant. Asterisks indicate the two-tailed level of significance: (\* <0.05, \*\* <0.025, \*\*\* <0.01).

	Female	Male
PDO (Oct-Feb)	0.14	-0.05
Hatchery pink/chum	0.25	0.15
NSEAK pink catch	0.01	0.22

Table 1.11: Models of male Gulf of Alaska growth and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	PDO	Hatchery pink/chum	NSEAK pink catch	AICc	R <sup>2</sup>
0.3017	-0.0009	5.13E-10	1.65E-09	-112.05	0.07
0.3005		5.07E-10	1.67E-09	-113.99	0.07
<b>0.3152</b>			<b>2.05E-09</b>	<b>-116.30</b>	<b>0.05</b>

Table 1.12: Models of female Gulf of Alaska growth and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	PDO	Hatchery pink/chum	NSEAK pink catch	AICc	R <sup>2</sup>
0.4087	0.0026	9.37E-10	-5.40E-10	-110.85	0.08
0.4034	0.0027	8.82E-10		-113.42	0.08
<b>0.4063</b>		<b>8.94E-10</b>		<b>-115.30</b>	<b>0.06</b>



Table 1.13: Correlation coefficients for analyses of relationships between saltwater plus growth, and environmental/biological indices. Values in bold font are statistically significant. Asterisks indicate the two-tailed level of significance: (\* <0.05, \*\* <0.025, \*\*\* <0.01).

	Female	Male
PDO (Oct-Feb)	0.09	<b>0.52**</b>
Hatchery pink/chum	<b>-0.42*</b>	-0.32
NSEAK pink catch	-0.23	-0.35

Table 1.14: Models of male marine plus (SWplus) growth and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	PDO	Hatchery pink/chum	NSEAK pink catch	AICc	R <sup>2</sup>
<b>1.4540</b>	<b>0.0124</b>	<b>-8.83E-10</b>	<b>-3.30E-09</b>	<b>-109.68</b>	<b>0.42</b>
<b>1.4290</b>	<b>0.0122</b>		<b>-3.97E-09</b>	<b>-110.86</b>	<b>0.38</b>
<b>1.3741</b>	<b>0.0126</b>			<b>-109.42</b>	<b>0.27</b>

Table 1.15: Models of female marine plus (SWplus) growth and AICc values.

The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	PDO	Hatchery pink/chum	NSEAK pink catch	AICc	R <sup>2</sup>
1.4430	0.0026	-1.89E-09	-1.86E-09	-92.44	0.17
<b>1.4470</b>		<b>-1.88E-09</b>	<b>-1.93E-09</b>	<b>-94.84</b>	<b>0.17</b>
1.4280		-2.07E-09		-96.77	0.15

Table 1.16: Correlation coefficients for analyses of relationships between average length-at-return and biophysical indices for males and females. Asterisks indicate the two-tailed level of significance: (\* <0.05, \*\* <0.025, \*\*\* <0.01).

	Male	Female
Early marine growth	0.06	0.37
Strait growth	-0.15	0.11
GOA growth	-0.16	0.05
Saltwater plus growth	<b>0.58**</b>	0.27
PDO (Oct-Feb)	<b>0.65***</b>	0.37
Dipac pink + chum	-0.25	-0.16
NSEAK pink catch	-0.25	-0.11
Size at return (Male)	NA	<b>0.68***</b>

Table 1.17: Models of average male length at return and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	MEM	MIS	MGOA	MPLUS	PDO	hatchery pink/chur\SEAK pink catch	AICc	R <sup>2</sup>
532.70	-130.80	111.90	-7.15	52.51	1.62	-1.22E-07	126.47	0.57
531.10	-131.90	113.90	-7.52	53.01	1.62	-1.24E-07	122.86	0.57
522.60	-123.90	110.30		56.34	1.57	-1.22E-07	119.70	0.57
473.10		111.10		52.02	1.51	-1.51E-07	118.41	0.56
<b>574.90</b>				<b>31.35</b>	<b>1.74</b>	<b>-1.27E-07</b>	<b>115.39</b>	<b>0.5337</b>
<b>620.20</b>					<b>2.15</b>	<b>-1.79E-07</b>	<b>114.88</b>	<b>0.5025</b>



Table 1.18: Models of average female length at return. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	FEM	FIS	FGOA	FPLUS	PDO	hatchery pink/churn\SEAK pink catch	AICc	R <sup>2</sup>
415.30	208.10	94.92	33.49	30.67	0.65	-1.39E-07	138.16	0.28
435.10	204.00	72.85	33.04	29.40	0.66	-1.08E-07	134.74	0.28
474.20	219.80		39.63	29.61	0.68	-7.74E-08	133.03	0.27
472.14	196.58		39.74	36.28	0.69		130.17	0.26
<b>551.79</b>			<b>36.67</b>	<b>41.65</b>	<b>0.99</b>		<b>126.94</b>	<b>0.2263</b>
<b>587.62</b>				<b>26.98</b>	<b>1.13</b>		<b>125.81</b>	<b>0.20</b>
623.89					1.20		125.42	0.1382

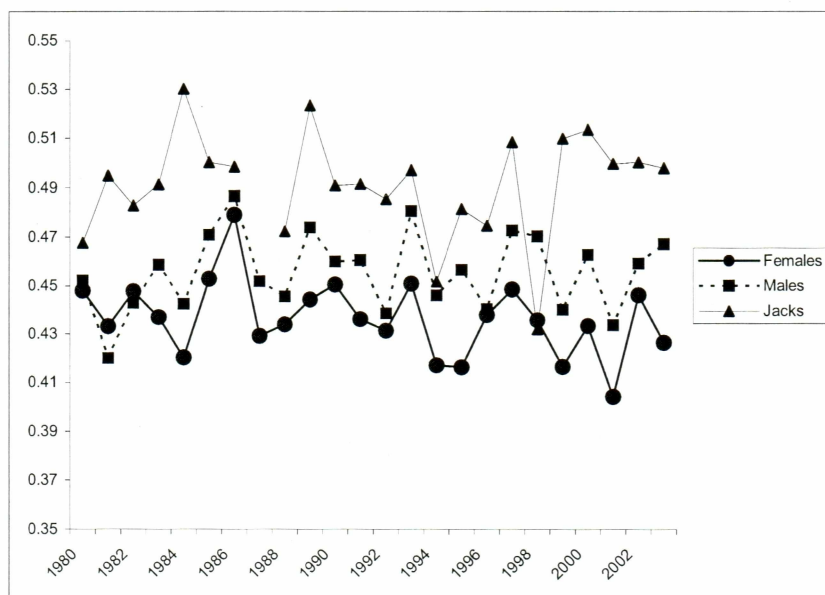


Figure 1.1: Early marine scale growth of Auke Creek coho salmon. Data are the average sum of marine circuli 1 – 7, over 20 sample scales.

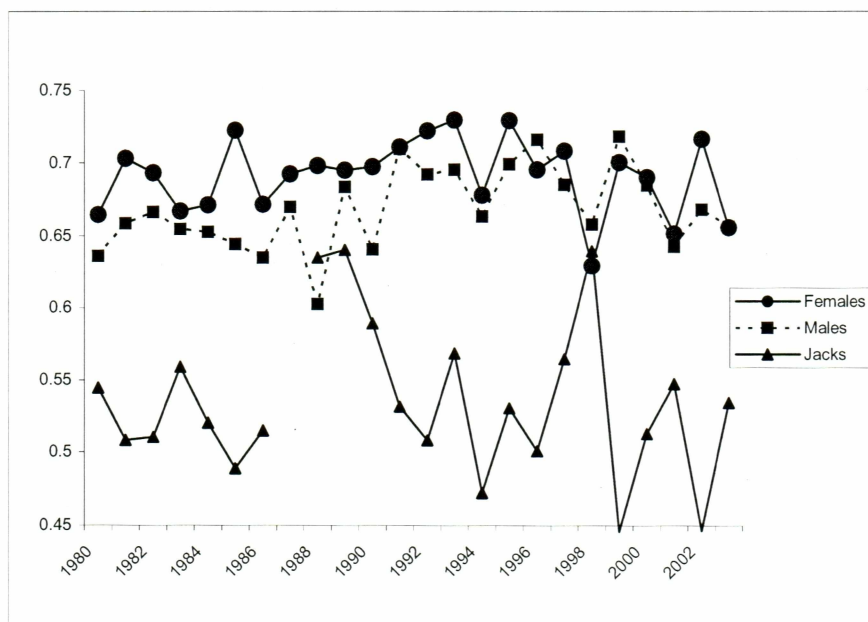


Figure 1.2: Strait habitat scale growth of Auke Creek coho salmon. Data are the average sum of marine circuli 8 – 20, over 20 sample scales. Jack growth diverges sharply because many individual jack scales have less than 20 circuli, resulting in smaller sums for the Strait habitat scale zone.

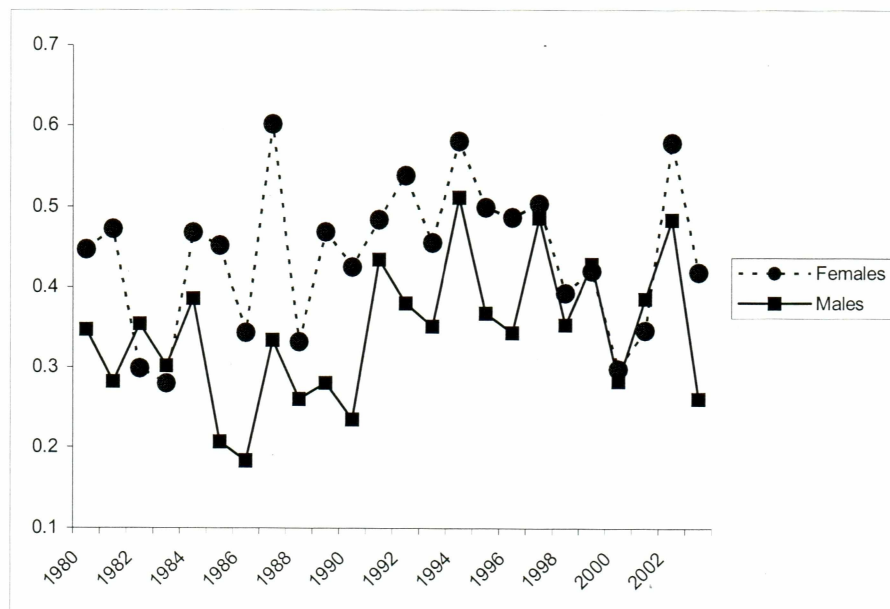


Figure 1.3: Gulf of Alaska scale growth of Auke Creek coho salmon. Data are the average sum of marine circuli 21 – annulus, over 20 sample scales.

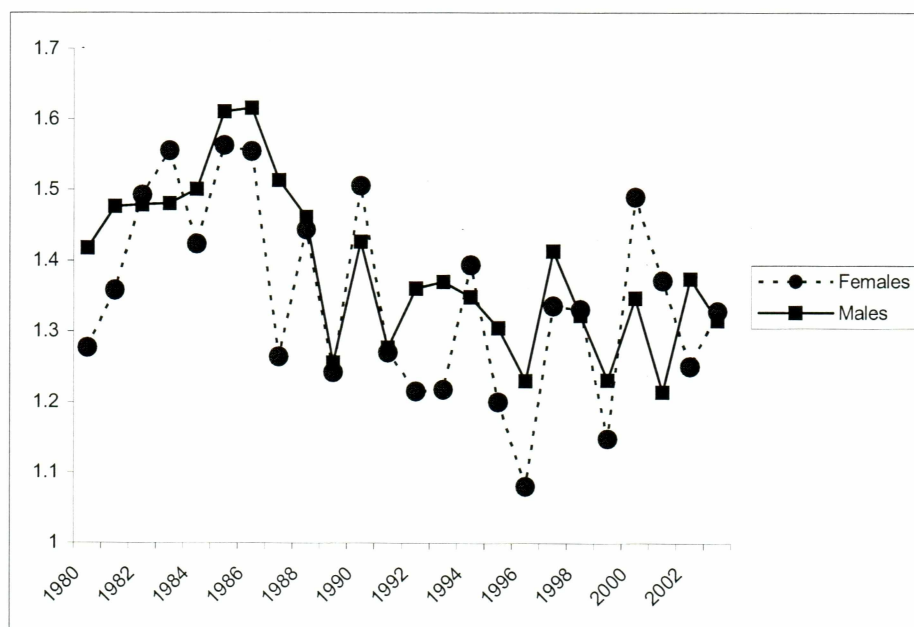


Figure 1.4: Saltwater plus (SW Plus) scale growth of Auke Creek coho salmon. Data are the average sum of marine circuli from the annulus to the scale edge, over 20 sample scales.



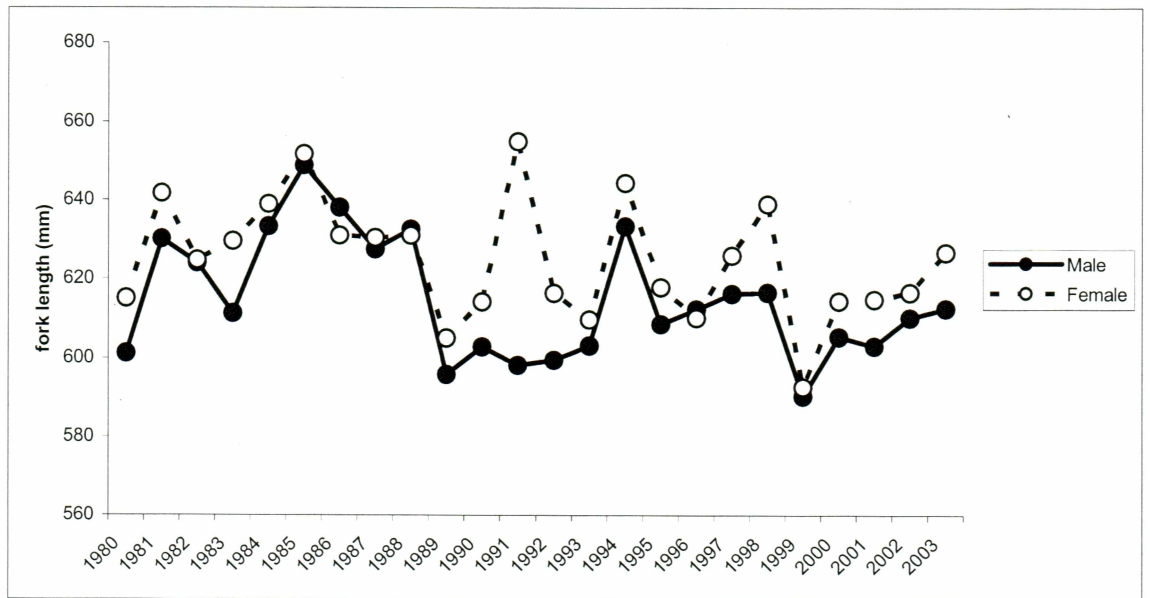


Figure 1.5: Average annual fork length of returned male and female Auke Creek coho salmon.

## **Chapter 2: Biophysical relationships with the marine survival of Auke Creek coho salmon.<sup>2</sup>**

### **Abstract**

Correlation analyses and stepwise regression analyses were used to investigate the effects of a suite of biophysical factors on the adult survival and jack return rate of Auke Creek coho salmon. Early marine growth was positively related to adult survival and jack return rate indicating size-selective mortality. Early marine indices of monthly SST and precipitation have stronger effects on jack return rate than on adult survival. The abundance of pink and chum salmon from a local hatchery had positive effects on adult survival and jack return rate. This may indicate that hatchery smolts represent prey resources for Auke Creek coho salmon during early marine residence, allowing increased growth and subsequent survival. The positive effect of hatchery smolts may also be due to predation buffering of Auke Creek coho salmon by pink and chum salmon.

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<sup>2</sup> Robins, J.B., M.D. Adkison, A.C. Wertheimer, and S.G. Taylor. 2006. Incorporating early marine growth into an analysis of biophysical factors influencing life-history specific survival of coho salmon from Auke Creek, Alaska. Prepared for submission in Transactions of the American Fisheries Society.

## Introduction

Biophysical conditions during the early marine residence of juvenile Pacific salmon (*Oncorhynchus*), have a significant impact on overall adult survival (Parker 1971; Bax 1983; Holtby et al. 1990; Pearcy 1992; Ryding and Skalski 1999; Beamish and Manhken 2001; Fukuwaka and Suzuki 2002). Large-scale climate indices such as the Pacific Decadal Oscillation and the Aleutian Low Pressure index are significantly related to salmon survival and productivity (Mantua et al. 1997; Hare et al. 1999; Koslow et al. 2002), but regional indices are more highly correlated with the survival of individual stocks (Adkison et al. 1996; Mueter et al. 2002). Mortality is often size-selective in salmon populations, and is regulated by early marine growth (Sogard 1997; Holtby et al. 1990). Predation is probably responsible for much of this size-selective mortality due to the improved ability of larger smolts to evade predators, but harsh winter conditions can also be a factor if smolts do not obtain sufficient energy resources to over-winter (Beamish and Mahnken 2001). Density of other species of salmon and forage fishes can affect growth and survival in different phases of the salmon marine residency (Holtby and Healey 1990; Ruggerone and Nielsen 2004).

This study investigates influences on the survival of Auke Creek coho salmon. The Auke Creek data set is the longest for a particular stock of coho salmon in Southeast Alaska. Survival of this stock varies greatly interannually (S.G. Taylor and Lum, J.L., unpublished report). The main objective of this study was an analysis of the importance of biophysical factors influencing survival of both adult and jack life-history types in this population. This analysis builds on that conducted by Briscoe et al. (2005).

## Methods

### Auke Creek adult and jack survival

Estimates of adult coho salmon survival were available for the years 1980 – 2003 (Figure 2.1; S.G. Taylor and J.L. Lum, unpublished report). Adult survival was estimated each year using the following formula:

$$s = \frac{(N_R + N_C)}{N_S},$$

where  $s$  is overall survival,  $N_R$  is adults that returned to the weir,  $N_C$  is the estimated number of adults caught in the fishery, and  $N_S$  is the number of smolts that emigrated two springs prior to the returns. Auke Creek coho salmon caught in the fishery are identified in the catch by presence of coded wire tags (CWTs), and the Alaska Department of Fish and Game uses these data to estimate the total catch of Auke Creek coho salmon. As adequate data on the sex ratios of smolts and adults are not available, males and females are lumped together in calculating adult survival.

Jack return rate was estimated similarly, by dividing the number of jacks that return to the weir by the number of smolts. The number of jacks caught in the fishery is negligible, since the fishery only targets adults. Because the proportion of smolts that will become jacks cannot be determined, jack survival is unobtainable. Jack return rate was influenced both by survival, and whether conditions favored selection of the jack life history (Gross 1985). The proportion of smolts that become jacks varies significantly between years.

One extreme outlier existed for both sets of estimates. Thus, adult survival and jack return rate data were normalized according to the following transformation:

$$p' = \arcsin(\sqrt{p})$$

where  $p$  is the survival and  $p'$  is the transformed survival.

### **Scale growth analysis**

Coho salmon scales have been collected and scale impressions on acetate cards taken from adult females, adult males and jacks at Auke Creek for the smolt years 1980-2003. Scales were not collected from jack males in 1987. A previous study created images and collected growth data from adult female scales (R. Briscoe, unpublished data). In 2005, under the same protocol, images of individual scales from adult males and jacks were generated using a microfiche reader with a ScreenScan scanning device connected to a desktop computer with ScreenScan software. Image contrast and resolution settings were set according to specifications recommended for coho salmon scales by the Alaska Department of Fish and Game Scale and Otolith Laboratory in Juneau, Alaska. A sample size of 20 scales per year was determined by power analysis. Sample sizes of 21-26 male and 15-25 jack scales were obtained for each year of the analysis (1980-2003), and 20 female scales were obtained for each year in a previous study (except 1980, for which only 14 scales were available) (R. Briscoe, unpublished data). The sample scales were selected non-randomly from available scales based on readability and scale condition. Scales in poor condition due to handling or regeneration were not used, as deformities and obscurities make circuli identification and measurement difficult or impossible. Condition of individual scales was determined based on visual inspection of scale shape (rounder scales allow the most accurate representation of somatic growth from circuli measurements), the clarity of the circuli, and the intactness of the scale's edge. Scale images were stored as digital files for subsequent analysis of growth patterns.



Adult male and jack scale growth measurements were generated following methods used for female scales (R. Briscoe, unpublished data). Scale growth was measured as the sum of the widths of scale increments (circuli). Because circuli are laid down progressively over time, the pattern of circuli widths represented on a scale can be used as a proxy for somatic growth rate (Fukuwaka and Kaeriyama 1997; Fisher and Pearcy 2005). The time schedule under which circuli are produced is not well understood; however, annual growth can be identified based on the presence of regions where circuli widths are narrow (annuli). During winter, somatic growth slows and circuli become narrower than in warmer months. To achieve finer temporal resolution of growth rate, a previous study (R. Briscoe, unpublished data) collected data from scales of juvenile coho caught in marine waters by SECM trawl sampling, and from those intercepted upon emigration from Auke Creek at the weir. Average circuli counts for juvenile coho salmon caught at each station were assumed to be representative of Auke Creek coho growth. Four zones of growth were identified by comparing circuli counts from scales obtained at the two stations: early marine growth, Strait habitat growth, Gulf of Alaska (GOA) growth, and saltwater plus (SW plus) growth. The average number of circuli from scales collected at Icy Strait (excluding freshwater growth) was classified as early marine growth, and the average number of circuli at the GOA stations was interpreted as Strait habitat growth combined with early marine growth. Since the number of juvenile coho caught per unit of effort drops off markedly after September (Orsi et al. 2000), the average number of circuli between the endpoint of strait growth (circulus 21) and the scale annulus was treated as GOA growth. Saltwater plus growth was defined as the region from the annulus to the scale edge. Early marine, Strait habitat, GOA, and SW plus growth zones were found to be represented by the following regions on the scale: marine circuli 1-7, circuli 8-20, circuli 21- the annulus, and the annulus to the scale edge, respectively.

Optimas 6.51 image analysis software, employing macros written by the Alaska Department of Fish and Game, was used to measure the widths of circuli of individual scales. The macros identify and mark circuli along the longest axis of a scale, as defined by the user. Misclassifications were manually corrected. Using an automated measurement process, circuli widths were determined and recorded. In order to reduce subjectivity in identification of annuli, an algorithm was devised to identify annuli from circulus width data; this was done by finding the local minimum circulus width within a range of circuli in which annuli are typically observed for this species and population. To reduce subjectivity due to observer differences, an algorithm was devised to find the circulus at which freshwater growth ends and saltwater growth begins by identifying a local maximum difference between averages of adjacent groups of three circulus widths within the array of circulus width data for an individual sample scale.

For individual scales, circuli widths in each zone were added to get zone widths, and then zone widths were averaged over all scale samples in each year to produce average annual zone widths. The scale growth data used in correlation analyses is average annual zone width, with values for all four zones available for all years in which scales were available.

### **Biophysical indices**

Several environmental and biological indices were compared to survival data. The environmental indices were: Auke Bay sea surface temperature (SST), Icy Strait air temperature, Auke Bay precipitation, and the Pacific Decadal Oscillation (PDO, winter sea surface temperature anomalies). The biological indices were: Macauley (DIPAC) hatchery releases of pink and chum salmon fry and Auke Creek coho salmon average smolt length.

### **Auke Bay sea surface temperature (SST)**

Daily SST measurements recorded at the Auke Bay dock (Wing et al. 2006) were averaged for the months of May and June for all years from 1979-2003. Regional SST may influence juvenile coho salmon indirectly by regulating productivity in marine waters and directly by increasing the growth potential of the fish at higher temperatures within their tolerance range (e.g., Brett (1969). Productivity can be nutrient-limited (Polovina et al. 1995).

### **Icy Strait air temperature index**

An index of air temperature was generated from data collected at Hoonah, Gustavus, and Elfin Cove and used as a proxy for SST in Icy Strait following the approach of Adkison et al. (1996). This index was created by subtracting the monthly mean air temperature over the years 1979-2002 (National Weather Service, <http://pajk.arh.noaa.gov/climatology/webcli.htm>) from monthly air temperatures for each year to obtain residuals. Residuals were then divided by the standard deviation of the monthly air temperatures for all years. This was performed for each of the three sites, for July, August, and September, the months during which juvenile salmon would be expected to inhabit strait habitat. Values for the three months were averaged for each site, and site values were again averaged to obtain the overall summer habitat air temperature index for Icy Strait (R. Briscoe, unpublished data). Icy Strait air temperature might be expected to positively affect survival if warmer conditions lead to improved growth, and mortality is size-selective.

### **Auke Bay precipitation**

The index for Auke Bay monthly precipitation was generated for the years 1979-2003 by measuring monthly total precipitation and averaging totals for each month over all years (Wing et al. 2006). Precipitation influences productivity in marine waters through formation of a freshwater lens, resulting in stratification of the water column (Mann and Lazier 1991). Stratification following mixing generally results in higher primary and secondary productivity. Because zooplankton are important food resources for juvenile salmon in marine regions, changes in their abundance can potentially affect rates of salmon growth and subsequent survival.

### **Pacific Decadal Oscillation (PDO)**

PDO index values are winter SST anomalies. For this study we used sums of the October-February North Pacific Ocean SST anomalies for the years 1980-2003, taken from Mantua et al. (1997) (<http://jisao.washington.edu/pdo/PDO.latest>). These months represent the initial period of Auke Creek juvenile coho salmon residence in the Gulf of Alaska, during which high pre-winter mortality due to cold and nutrient-poor conditions would be expected (Beamish and Mahnken 2001). Because the PDO index incorporates data for the entire North Pacific Ocean, it represents temperature conditions on a large spatial scale.

### **Abundance of DIPAC hatchery pink and chum fry**

The number of pink and chum salmon fry produced each year at the DIPAC hatchery, which is located only a few kilometers from Auke Creek in Juneau, Alaska, are estimated prior to release into marine waters (R. Focht,



unpublished data). The abundance of these pink and chum fry could be negatively correlated with the survival of Auke Creek coho salmon under size-selective mortality due to density-dependent competition for food resources and reduced growth. It also could be positively correlated with Auke Creek coho survival if hatchery fry serve as a buffer to predation upon Auke Creek smolts, or if hatchery fry add to the available food resources of Auke Creek coho juveniles, allowing improved growth.

### **Auke Creek coho smolt length**

Fork lengths of all Auke Creek coho smolts are measured at the weir on Auke Creek each year. The length of coho smolts upon emigration from Auke Creek may influence subsequent growth. Other studies have documented the influence of size on survival in salmonid fishes (Sogard 1997). In general, theory holds that fish of larger size will be more successful in avoiding predators, and larger smolts generally survive better than smaller smolts emigrating at the same time (Bilton et al. 1982; Holtby et al. 1990; Lum 2003). Smolt size is not necessarily correlated with adult size. In the jack life history, smolts that become jacks initially grow fast and are larger as smolts, but as mature jacks are small in relation to mature adults (Rowe and Thorpe 1990; Lum 2003).

### **Auto-correlation and normality of data**

All data sets were tested for lag 1 auto-correlation to determine whether tests of significance required correction (Pyper and Peterman 1998). Data sets were also examined for normality using visual inspection of frequency histograms and P-P plots, and corrected if necessary.

## **Correlation Analyses and Model Selection**

Following Briscoe et al. (2005) we performed correlation analyses for Auke Creek coho adult and jack survival with all of the biophysical variables, then conducted a model selection process using AICc (Corrected Akaike Information Criterion) to assess which combinations of predictor variables produced the optimum models of survival.

In this analysis, parameters for early marine scale growth of males, females, and jacks, and Strait habitat scale growth of males and females were added to correlation analyses and full models of Auke Creek coho overall adult survival and jack return rate. “Strait habitat growth” of jacks likely represents growth closer to Auke Creek because jacks have a limited marine residence time. Model selection was conducted by comparing the AICc values between individual models with different combinations of variables.

### **Correlation analyses**

Correlation analyses were performed to examine relationships of Auke Creek coho adult survival and jack return rate with biophysical indices and Auke Creek salmon early marine growth. This was done only for those cases where a biologically plausible mechanism existed for the effect of a variable on survival. Peterson correlation coefficients were calculated using the Correl() function in Microsoft Excel, and statistical significance was assessed using critical values of the correlation coefficient  $r$  (Zar 1999). Outliers were identified and visually examined to eliminate the potential for erroneous results.



## Model Selection

Model selection was conducted using multiple regression models to examine the relationship of biophysical parameters to Auke Creek coho salmon adult survival and jack return rate. To test the effects of environmental and biological phenomena on the response variables of interest, corrected Akaike Information Criterion (AICc) values were calculated for all possible models for a given response variable. AICc values were calculated as:

$$AIC + \frac{2P(P+1)}{N-P-1},$$

where AIC is determined by the following formula:

$$AIC = N * \log(RSS/N) + 2P + \text{constant}$$

where RSS is the residual sum of squares of the model, N is the number of samples, and P is the number of parameters in the model.

The best model was identified as that having the lowest AICc value. Other models with an AICc within 2 are almost equally plausible (Burnham and Andersen 2002). AICc is used instead of the uncorrected AIC statistic in situations where sample sizes are low.

The response variables of interest in this case were adult survival and jack return rate. The full model for adult survival was:

$$s = \alpha + \beta G_{MEM} + \beta G_{MIS} + \beta G_{FEM} + \beta G_{FIS} + \beta T_M + \beta T_J + \beta P_M + \beta P_J + \beta D_{PC} + \beta L_S$$

where  $G_{MEM}$  and  $G_{MLS}$  are male early marine and Strait habitat growth respectively,  $G_{FEM}$  and  $G_{FIS}$  are female early marine and Strait habitat growth respectively,  $T_M$  and  $T_J$  are Auke Bay sea surface temperature in May and June respectively,  $P_M$  and  $P_J$  are Auke Bay precipitation in May and June respectively,  $D_{PC}$  is the abundance of pink and chum salmon fry released from DIPAC hatchery, and  $L_S$  is the average fork length of emigrating smolts. The full model for jack return rate was:

$$s = \alpha + \beta G_{JEM} + \beta T_M + \beta T_J + \beta P_M + \beta P_J + \beta D_{PC} + \beta L_S$$

where  $G_{JEM}$  is jack early marine growth,  $T_M$  and  $T_J$  are Auke Bay sea surface temperature in May and June respectively,  $P_M$  and  $P_J$  are Auke Bay precipitation in May and June respectively,  $D_{PC}$  is the abundance of pink and chum salmon fry released from DIPAC hatchery, and  $L_S$  is the average fork length of emigrating smolts.

Stepwise model selection was performed using the “step” and “lm” functions in the statistical software package R (CRAN project; <http://cran.r-project.org/>). The R procedure is based on the AIC statistic; models selected using R were examined to ensure that they would have also have been selected using the AICc criterion.

## Results

### Correlation analyses: adult survival

For the period from 1980-2003, adult survival of Auke Creek coho salmon was positively correlated with both male early marine and strait growth (Table 19). Early marine growth of males explained 16% of the variation in adult

survival (Figure 2.2). Female early marine growth and strait growth were also positively correlated with adult survival, but these correlations were weaker and not statistically significant; early marine growth of females explained less than 1% of the variation in adult survival (Figure 2.3). No significant relationships were detected for males or females between Gulf of Alaska or saltwater plus growth and adult survival. The abundance of hatchery pink and chum salmon had a significant positive relationship with adult survival. Indices of sea surface temperature in Auke Bay and Icy Strait, as well as the index of the PDO were positively, but not significantly correlated with adult survival. Indices of Auke Bay precipitation were negatively, but not significantly correlated with adult survival (Table 19).

#### **Model selection: adult survival**

The best model of adult survival contained a single variable: the abundance of DIPAC hatchery pink and chum releases. This single variable accounted for 44% of the variation in survival. Two other models were equally good: a model incorporating an additional parameter for male early marine growth, and a model incorporating additional parameters for both male and female early marine growth. In the latter, the effect of male early marine growth on survival was positive, while that of female early marine growth was negative (Table 20). These two models increased the variation in adult survival explained to around 50%.

#### **Correlation analyses: jack return rate**

Jack return rate was not significantly correlated with jack early marine growth. However, jack return rate showed a strong positive correlation with jack strait growth (Figure 2.4). Jack return rate was positively and significantly related

to Auke Bay SST in both May and June, and positively, but not significantly related to Icy Strait air temperature and the PDO index. Jack return rate was negatively, but not significantly related to the indices of precipitation in Auke Bay. A significant positive correlation was detected between Auke Creek average smolt size and jack return rate (Table 19).

### **Model selection: jack return rate**

The best model of jack survival contained four variables: May and June Auke Bay precipitation, the abundance of DIPAC hatchery pink and chum releases, and average Auke Creek smolt length. Two other models were equally good: a model including an additional parameter for jack early marine growth, and a model including additional parameters for both jack early marine growth and June SST (Table 21). These models explained 70% to 76% of the variation in jack return rate.

## **Discussion**

Auke Creek coho salmon adult survival was positively related to the early marine growth of males and females, as well as to pink/chum hatchery release abundance. The positive effect of early marine growth on the adult survival of Auke Creek coho salmon indicates that survival is size-selective in this population. This is typical for many populations of Pacific salmon (Sogard 1997; Holtby et al. 1990; McGurk 1996; Beamish and Mahnken 2001). Holtby et al. (1990) showed that Carnation Creek (British Columbia) coho salmon survival was size-dependent during years of poor growing conditions in the marine environment. Willette et al. (2001) showed that survival of pink salmon in Prince



William Sound, Alaska is mediated by size when food abundance levels require foraging in regions with higher predator abundances. The “critical size/critical period hypothesis” (Beamish and Mahnken 2001) holds that survival improves after a fish reaches a critical size, due to the concomitant increase in the ability to evade predators, and the increased ability to survive harsh winters during which food is scarce and temperatures are extremely cold. The opposite pattern, in which smaller individuals have a survival advantage, is rare (Fisher and Pearcy 1988).

The positive effect of hatchery pink and chum salmon smolt abundance on adult survival of Auke Creek coho salmon indicates that the abundance of potential prey resources may be a mechanism for regulating early marine growth and size-selective mortality in coho salmon. In an analysis of multiple regression models, hatchery pink and chum salmon abundance was positively, but not significantly related to early marine growth of Auke Creek coho salmon (J.Robins, unpublished data). Juvenile coho salmon are known predators of juvenile pink salmon and can capture prey that are more than half their own length (Hargreaves and LeBrasseur 1985, 1986). This predator-prey relationship would be expected to change after the first few weeks in the marine environment since pink salmon grow faster than coho salmon, and most likely become large enough to avoid predation by them (Godin 1981).

It is possible that the positive effect of hatchery pink and chum salmon juvenile abundance on Auke Creek adult coho salmon survival during early marine residence does not involve growth as a mechanism regulating mortality. Hatchery smolt abundance may allow increased coho smolt survival by acting as a buffer to predation on coho salmon smolts in Auke Bay, during the short time that both the wild and hatchery smolts inhabit the same regions prior to seaward migration (Briscoe et al. 2005). Because the hatchery juveniles are fed prior to release, they are larger and thus less susceptible to predation by coho salmon smolts than their wild conspecifics. Pink salmon are typically smaller and less

risk-averse than other juvenile salmon species in the early marine phase, feeding diurnally at the surface (Godin 1984) which may increase their vulnerability to predation, yet they also grow faster than other salmon species (Godin 1981). Auke Creek coho salmon growth in the Gulf of Alaska and upon return is negatively related to the abundance of hatchery pink and chum salmon, and to pink salmon catch in Northern Southeast Alaska (J.Robins, unpublished data). The positive effect of hatchery juvenile salmon abundance on coho salmon early marine growth may become negative when the hatchery fish reach sizes large enough to begin feeding at a higher trophic level, thus potentially competing more directly with coho salmon for available prey. Pink salmon abundance has been shown to negatively affect the growth and survival of other salmon populations (Ruggerone et al. 2003; Ruggerone and Nielsen 2004).

Auke Creek coho jack return rate was positively related to early marine growth of jacks, as well as to regional biophysical conditions, and smolt length. The positive effect of jack early marine growth on the return rate of jacks implies that mortality of jacks is size-selective. However, it could also indicate that higher growth rates induce more juvenile male coho salmon to mature as jacks. Because jacks most likely do not migrate into Icy Strait, "Strait habitat growth" of jacks is probably a representation of growth closer to Auke Creek. Significant positive correlations between "Strait habitat growth" of jacks, but not early marine growth imply that it was during the latter part of jack early marine residence that growth was most significantly related to jack return rate. Auke Creek coho jacks spend only one summer in the marine environment before returning to spawn. It is unlikely that jacks travel great distances during these few months since consumption rate and swim speed are limited by metabolism and size (Brett 1983; Quinn 1988).

The positive effect of regional biophysical conditions on jack return rate supports the hypothesis that the marine migration of jacks is limited to areas close to their natal stream, while adults move offshore after a short period of time



(Briscoe et al 2005). Early marine growth of jacks is positively related to regional biophysical conditions (J. Robins, unpublished data), providing further support for this hypothesis. The positive effects of SST and precipitation on jack growth are in accordance with these expectations (Briscoe et al. 2005). Auke Bay SST was positively and significantly correlated with jack return rate, but not with adult survival. As was the case for adult survival, the positive effect of hatchery pink and chum salmon abundance on jack return rate indicates that pink and chum salmon may represent prey resources for coho jacks, or that the juvenile hatchery fish buffer the jack-type coho salmon from predation. Although Auke Creek coho jack growth was not significantly related to jack return rate, the average size of Auke Creek coho smolts was positively and significantly related to jack return rate.

The negative relationships between Auke Bay precipitation and both jack return rate and adult survival are opposite to the hypothesized effects. The interpretation of this result is unclear. One possibility is that the link between precipitation and productivity may not be direct enough to cause a signal in the return rates of Auke Creek coho salmon. Also, spring productivity in a subarctic marine embayment like Auke Bay may be high enough that the variation will be independent of effects on growth and survival of juvenile coho salmon.

The average length of Auke Creek coho smolts upon emigration to marine waters is positively related to the jack return rate, but not to interannual variation in adult survival rate. Due to the constraints of their life history and limited marine migration, jacks may endure different predator regimes than adult-type juvenile coho salmon that likely move offshore shortly after entering the marine environment. This could explain why smolt size appears to be of greater importance for survival of jacks than for adults. Alternatively, in years of good growth, more males may return as jacks, positively influencing jack return rate. Jacks typically grow faster than adult-type smolts (Silverstein and Hershberger 1999; Larsen et al 2004; Vollestad et al 2004), and larger smolts in this population

of coho salmon become jacks at maturity more frequently than small smolts (Lum 2003).

Briscoe et al. (2005) showed that the survival of Auke Creek adults and the return rate of jacks were positively and significantly correlated (Figure 2.1). Because adults and jacks are sympatric only during the early marine phase of the adult life history, this result implied that factors regulating adult survival occur during the first few months of juvenile marine residence. However, because jack survival only explained 37% of the variation in adult survival, mortality in other marine life history phases must be important in controlling overall adult survival (Briscoe et al. 2005). Mortality in juvenile salmon may be regulated by “top-down” or “bottom-up” processes, both in the form of size-selective mortality due to predation or to competition and condition factor, respectively (Holtby et al. 1990; Beamish and Mahnken 2001; Willette 2001). Growth of Auke Creek juvenile coho salmon in Strait habitat was positively correlated with survival for males, but was not significantly correlated for females. The best models of adult survival did not include a parameter for Strait habitat growth, implying that it did not have a significant effect on overall adult survival. Icy Strait air temperature was positively, but not significantly correlated with adult survival. Additional mortality undoubtedly occurs while coho salmon are at sea due to factors such as predation and disease.

Large-scale environmental indices are significantly related to salmon survival and productivity in many cases (Beamish and Bouillon 1993; Adkison et al. 1996; Mantua 1997; Hare et al. 1999; Koslow et al. 2002), but regional indices are typically more highly correlated with survival and productivity of individual populations (Mueter et al. 2002). Positive correlations between adult survival of Auke Creek coho salmon and survival of two other coho salmon populations in close proximity to Auke Creek were detected by Briscoe et al. (2005), implying regional similarities in the mechanisms regulating survival. Auke Creek coho salmon survival was significantly correlated with commercial coho salmon

fishery catch abundances in southeast Alaska, and in northern southeast Alaska, implying the influence of large-scale mechanisms regulating productivity of salmon in southeast Alaska (Briscoe et al. 2005).

A limitation of this study is that the survival data used in this analysis is not sex-specific, and therefore may not be representative of the survival rates of males or females separately. While growth data for males and females and overall adult survival data is available for the Auke Creek coho salmon population, sex ratio data of returns and smolts is not. While all adults returning to Auke Creek are enumerated, only subsamples of the return are sexed and measured. Because sampling of returning adults at the Auke Creek weir is non-random, the proportion of males and females in the returned adults is not accounted for. Smolts cannot be identified to sex by visual inspection. As a result, it is not possible to detect differences in male and female survival. Previous studies have shown there is no reason to expect differences from a sex ratio of 50:50 in smolts (Dittman et al. 1998; Spidle et al. 1998), though differences in the sex ratio of adult returns have been observed (Holtby and Healey 1990). Auke Creek coho salmon have sex-specific differences in size at return, variation in size at return, and growth rates in certain marine habitats, indicating differences between males and females in foraging behavior (J. Robins, unpublished data). Sex-specific differences in foraging strategy may cause differences in survival between males and females (Holtby and Healey 1990).

The results of this study indicate that both male and female early marine growth have significant positive effects on overall adult survival, and that jack early marine growth positively affects jack return rate. Early marine SST and precipitation have a stronger influence on jack return rate, than on adult survival. The abundance of pink and chum salmon from a local hatchery have a positive effect on adult survival, but no effect on jack return rate.

If possible, future analyses should attempt to incorporate scale growth data from juvenile Auke Creek coho in order to strengthen these results. Incorporating



indices of primary and secondary productivity to correlation analyses and model selection would also benefit the overall understanding of relationships between regional biophysical factors and Auke Creek coho salmon survival. Because Auke Creek coho salmon are an indicator stock for the Alaska Department of Fish and Game, these results will contribute to an ongoing effort to manage stocks based on information about the mechanisms controlling marine mortality.

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Table 2.1 : Correlation coefficients for analyses of relationships between zonal scale growth and survival/return rates of Auke Creek coho adults and jacks.

Values greater than 0.40 are significant at  $\alpha=0.10$ . Asterixes indicate the two-tailed level of significance:

(\* <0.05, \*\* <0.025, \*\*\* <0.01).

		Adult survival	Jack return rate
Female	Early marine	0.05	na
	Strait	0.31	na
	GOA	-0.03	-0.13
	SW plus	-0.14	-0.17
Male	Early marine	<b>0.40*</b>	na
	Strait	<b>0.43*</b>	na
	GOA	0.11	-0.01
	SW plus	-0.28	-0.12
Jack	Early marine	na	0.00
	Strait	na	0.42
	AB May SST	0.29	<b>0.63***</b>
	AB June SST	0.17	<b>0.46*</b>
	AB May Precip	-0.10	-0.24
	AB June Precip	-0.01	-0.19
	Icy Strait AT	0.17	0.22
	PDO (Oct-Feb)	0.15	0.23
	Hatchery pink/chum	<b>0.66***</b>	<b>0.64***</b>
	Smolt length	0.16	<b>0.47**</b>

Table 2.2: Models of adult survival and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	FEM	FSTR	MEM	MSTR	May SST	May precip	June SST	June precip	Pink/chum	Smolt length	AICc	R <sup>2</sup>
-1.0820	-2.4850	1.1080	2.8020	-0.1661	-0.0280	-0.0141	0.0287	0.0047	1.77E-09	0.0050	-105.567	0.608
-1.0540	-2.2720	0.9696	2.6860		-0.0263	-0.0137	0.0250	0.0036	1.75E-09	0.0046	-111.563	0.607
-1.0680	-2.2570	1.0040	2.6490		-0.0260	-0.0155	0.0219		1.72E-09	0.0051	-116.67	0.605
-0.4119	-1.8660	0.6651	2.4170		-0.0194	-0.0114	0.0222		1.89E-09		-120	0.583
0.0706	-1.3690		1.9940		-0.0165	-0.0091	0.0149		2.26E-09		-122.639	0.558
0.2157	-1.2470		1.9100		-0.0124	-0.0083			2.25E-09		-125.347	0.541
0.0496	-1.1440		2.0020		-0.0072				2.08E-09		-127.685	0.524
<b>0.0057</b>	<b>-1.0590</b>		<b>1.8680</b>						<b>1.91E-09</b>		<b>-130.13</b>	<b>0.514</b>
<b>-0.1458</b>			1.1770						2.01E-09		<b>-131.529</b>	<b>0.489</b>
<b>0.3818</b>									2.23E-09		<b>-131.608</b>	<b>0.437</b>



Table 2.3: Models of jack survival and AICc values. The lowest AICc values within 2 units of one another are in bold to indicate the best models.

Intercept	JEM	May SST	May precip	June SST	June precip	Pink/chum	Smolt length	AICc	R <sup>2</sup>
-0.7338	0.4280	-0.0047	-0.0117	0.0121	-0.0120	8.13E-10	0.0051	-156.80	0.7718
<b>-0.7711</b>	<b>0.4492</b>		<b>-0.0133</b>	<b>0.0139</b>	<b>-0.0118</b>	<b>9.14E-10</b>	<b>0.0055</b>	<b>-159.36</b>	<b>0.7628</b>
<b>-0.6296</b>	<b>0.3473</b>		<b>-0.0146</b>		<b>-0.0136</b>	<b>9.35E-10</b>	<b>0.0065</b>	<b>-159.89</b>	<b>0.7288</b>
<b>-0.4083</b>			<b>-0.0132</b>		<b>-0.0117</b>	<b>9.71E-10</b>	<b>0.0060</b>	<b>-160.98</b>	<b>0.7026</b>
-0.3634			-0.0083			1.02E-09	0.0050	-156.84	0.5958
-0.3662						1.01E-09	0.0047	-155.05	0.5102
0.1637						1.14E-09		-153.15	0.4051

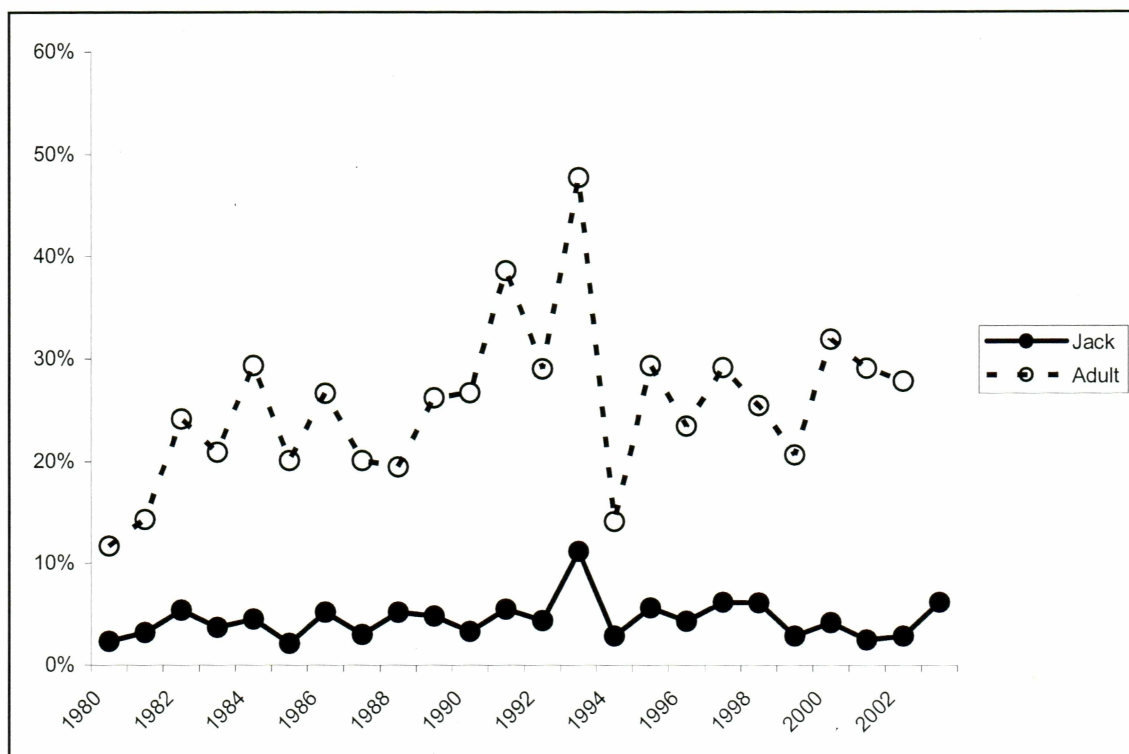


Figure 2.1: Time series (1980-2003) of adult survival and jack return rate of Auke Creek coho salmon.

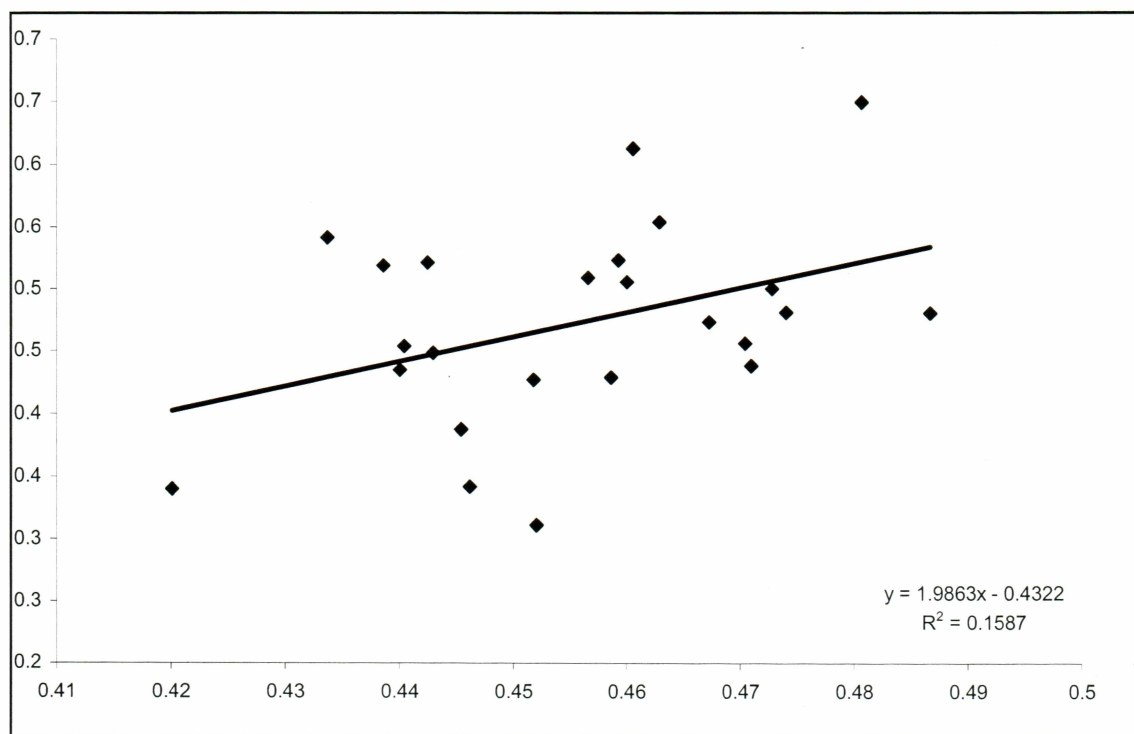


Figure 2.2: Scatterplot of Auke Creek coho adult survival (y-axis) and Auke Creek coho male early marine growth.

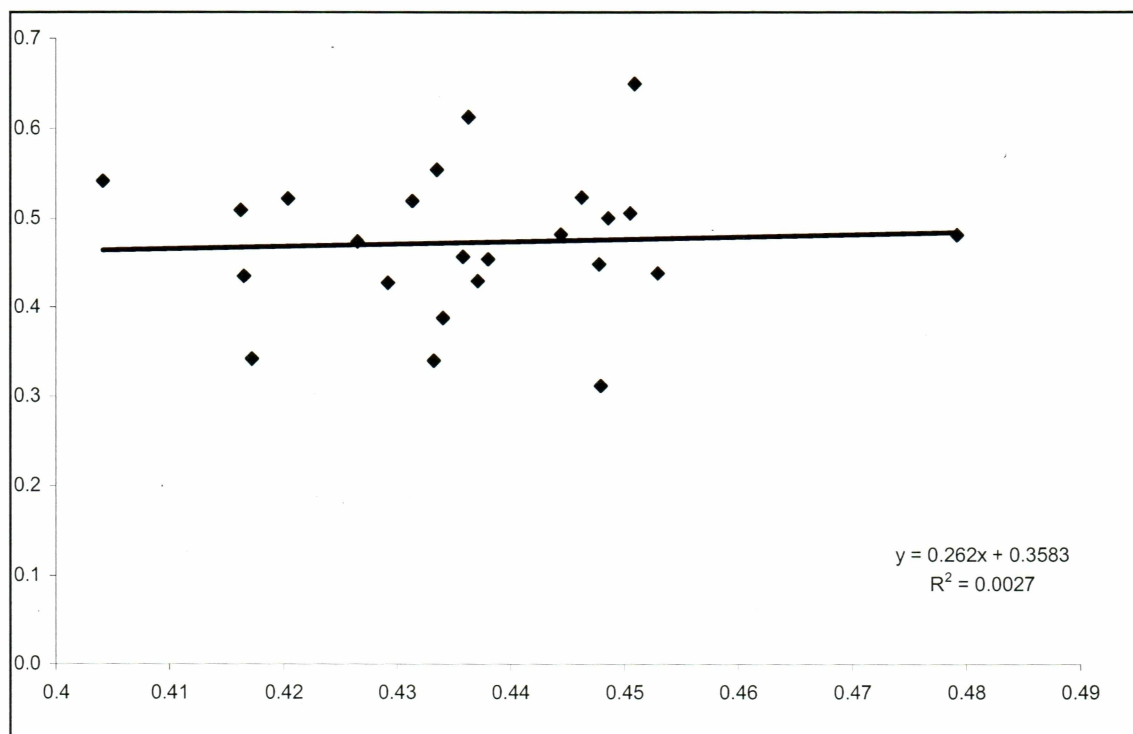


Figure 2.3: Scatterplot of Auke Creek coho adult survival (y-axis) and Auke Creek coho female early marine growth.

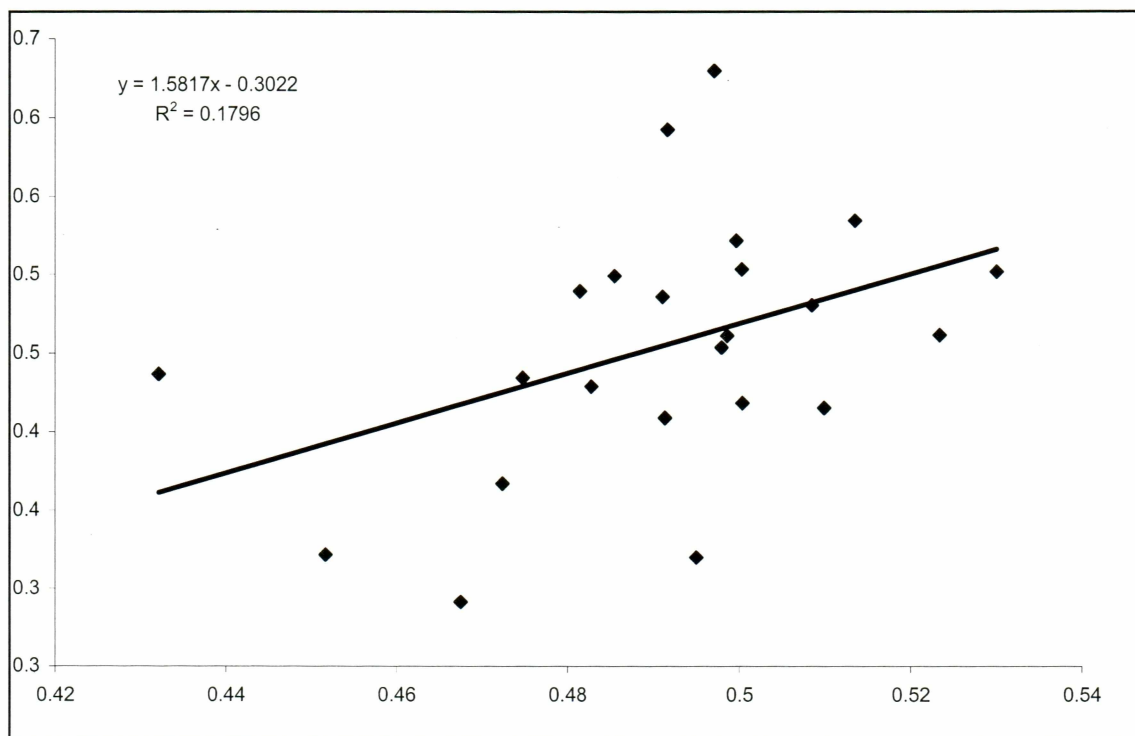


Figure 2.4: Scatterplot of Auke Creek coho jack return rate (y-axis) and Auke Creek coho jack early marine growth.



## General Conclusions

This thesis produced several conclusions about relationships between biophysical conditions, marine growth, and overall survival of Auke Creek coho salmon. Early marine growth of adult-type coho salmon was not related to that of jack-type coho salmon in this population. Biophysical conditions in Auke Bay were more closely related to early marine growth and return rate for jack-type coho salmon, than for adult-type coho salmon. Auke Creek coho salmon growth in Icy Strait was negatively related to air temperature in Icy Strait, but in the Gulf of Alaska was positively related to the index of the Pacific Decadal Oscillation. Indices of pink salmon abundance were positively related to early marine growth of jacks, but not to that of adults, and negatively related to late ocean growth of adults. The abundance of hatchery pink and chum salmon appeared to affect adult survival positively, but had no effect on the return rate of jacks. Indices of hatchery pink and chum salmon abundance were negatively related to the average size-at-return of male and female Auke Creek coho salmon. However, the abundance of pink salmon caught in Northern Southeast Alaska was negatively related to the size-at-return of Auke Creek coho males, but positively related to that of females, implying potential differences in foraging between sexes. Female average size-at-return was consistently greater than that of males, and exhibited significantly less variation annually. Both male and female early marine growth of Auke Creek coho salmon had significant effects on adult survival, and jack early marine growth positively affected jack return rate. The abundance of pink and chum salmon from a local hatchery appeared to have positive effects on both adult survival and jack return rate.